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THE LIFE HISTORY OF POLYSIPHONIA VIOLACEA.

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SHIGEO YAMANOUCHI.

(WITH THREE DIAGRAMS AND PLATES XIX–XXVIII)

INTRODUCTION.

THERE have been published by various authors many accounts of investigations on the red algae treating of the morphology of the thallus, the development of the cystocarp, and tetraspore formation. The first general studies on the reproductive processes in the group were those of BORNET and THURET (**12**) and JANCZEWSKI (**43**). These papers have never been surpassed in clearness of expression and beauty of illustration, but they considered simply the outer morphology or histology and gave no cytological details of fertilization, nor did they trace the life history. SCHMITZ (**69**) published an account of the fructifications of more than forty species in various groups of the red algae, giving special attention to the auxiliary cells, but in his conclusions he failed to distinguish between the act of fertilization and the secondary fusions concerned with the auxiliary cells, and he developed elaborate speculations in which these fusions were included as a part of the sexual process. This misconception was cleared up by OLTMANNS' discovery (**55**) that the real sexual act is the union of male and female gamete nuclei in the carpogonium, and that the auxiliary cells are probably only concerned with the nourishment of the cystocarp. OLTMANNS was the first author to develop the theory that the structure derived from the fertilized carpogonium was sporophytic in character; however, he presented no

cytological evidence for this view. WOLFE (**86**) placed this theory of OLTMANNS on a cytological basis by showing that the cystocarp of Nemalion contained nuclei with double the number of chromosomes found in the sexual plants or gametophytes. However, WOLFE did not give a detailed account of the period of chromosome reduction. Nemalion is one of the simplest types of the red algae. There are no auxiliary cells or tetraspores, at least on the American plants so far as known; consequently the life history is very much simpler than that of the higher forms. The behavior of the auxiliary cell nucleus during the development of the cystocarp has been studied by OLTMANNS (**55**) with especial clearness in Callithamnion and Dudresnaya, but the structural difference between the nuclei of auxiliary cells (gametophytic) and those derived from the fertilized carpogonium (sporophytic) was not determined by him. Moreover, as regards the real nature of the tetraspore, so characteristic of the red algae, there has been no cytological work except a study of nuclear division in Corallina by DAVIS (**18**).

The significance of the tetraspore in the life history was not known. Various authors have presented speculations upon the subject; for example, OLTMANNS (**55**) regarded the tetraspore as an asexual reproductive structure comparable to brood organs or gemmae, having no fixed place in the life cycle, and STRASBURGER has followed this interpretation.

This investigation was begun in the hope that some of these problems might be solved by carefully following the life history of a type with particular attention to the behavior of the nucleus at critical periods. Although red algae include a wide range of types, the nature of the tetraspore and the history of the life cycle where tetraspores are present have probably been determined by this investigation of the ontogeny of *Polysiphonia violacea* Grev., except in forms where abnormalities may be present, due perhaps to apogamy or apospory.

As stated in a preliminary paper (YAMANOUCHI **87**), the material was collected at Woods Hole, Mass., during July and August 1905, where cultures of the carpospores and tetraspores were made to obtain stages in their germination. The method of killing, fixing, imbedding, cutting, and staining are given in that preliminary note.

This paper presents first the results of my studies of the mitosis in

germinating tetraspores and carpospores and in the vegetative cells of mature plants; then comes an account of spermatogenesis, formation of procarp, fertilization, and development of the cystocarp; tetraspore formation is then considered, followed by a description of certain abnormalities; finally, there is a discussion of the cytological phenomena and alternation of generations. This last topic has been given considerable attention, for the chief results of this investigation have been the establishment of an antithetic alternation of generations in Polysiphonia, with the period of chromosome reduction at the time of tetraspore formation.

The investigation was begun during the summer of 1905 at the suggestion of Dr. BRADLEY M. DAVIS during my stay as an occupant of a Carnegie research table at the Marine Biological Laboratory, Woods Hole; and to the Carnegie Institution I wish to express my obligations for the privilege of the table. The studies were continued and completed by me in the Hull Botanical Laboratory as a Fellow of The University of Chicago, under the direction of Professor JOHN M. COULTER and Dr. CHARLES J. CHAMBERLAIN, the kind assistance and painstaking criticism of Dr. DAVIS continuing also throughout the whole progress of the investigation. To these gentlemen I am under great obligation; and also to the other members of the botanical staff of Hull Botanical Laboratory for courtesies extended to me in many ways.

THE FIRST MITOSIS IN THE GERMINATING TETRASPORE.

The tetraspore when discharged from the parent plant assumes a spherical form. Plastids usually lie near the periphery of the cell, whose cytoplasm presents an irregular, coarse alveolar structure, with the nucleus lying near the center. The cytoplasm surrounding the nuclear membrane is a finer network than anywhere else in the cell. Within the nucleus there is a very delicate linin mesh dotted here and there with chromatic granules (*fig. 1*). From the fact that the transverse walls of the cytoplasmic alveoli end on the nuclear membrane at points where the linin threads start, it seems possible that there exists a close physiological relation between these structures. The nucleus generally contains a single nucleolus, variously situated and homogeneous in structure, but sometimes two nucleoli are present.

Preliminary to mitosis, the delicate network becomes somewhat coarser and the thread somewhat broader, and gradually in many different parts the chromatin granules appear in irregular rows as chains of beads of different lengths. There are about 20 of these chains, as illustrated in *figs. 2a–2c*, which represent three sections of the same nucleus. They are the beginnings of the chromosomes, similar to the prochromosomes described by OVERTON (**58**) in the presynaptic stage in the pollen mother cells of Thalictrum and three other species of flowering plants. The material which accumulates in these prochromosomes must come from the chromatin granules imbedded in the linin thread, for it is evident that the nucleolus does not contribute any material directly to their formation. This behavior is therefore similar to the process of chromosome formation in higher plants, and is very different from the condition reported by WOLFE (**86**) for Nemalion, where the chromosomes are described as coming out from the nucleolus. The nucleolus of Polysiphonia remains unchanged while the prochromosomes are being formed. These prochromosomes gradually become more pronounced, increase in breadth, and the bead-like structure is transformed into the more homogeneous rod-shaped chromosomes that become distributed through the whole nuclear cavity attached to a linin thread, as shown in *figs. 3a* and *3b*, which represent two sections of the same nucleus. The nucleolus may remain undivided or fragment into two at this time.

The cytoplasm around the resting nuclear membrane appears at first homogeneous, but during prophase there is a gradual accumulation on the two opposite sides of the nucleus, and finally two deeply staining centrosome-like bodies appear, forming the poles of the more slightly elongated nucleus (*fig. 4*). While these changes in the cytoplasm are going on without the nucleus, some important events take place within. The chromosomes become thickened and more compact and gather in the middle region of the nuclear cavity, with linin threads still attached to their ends, and at last they are arranged in the equatorial plate (*fig. 5*). The nuclear membrane is still present when the spindle is developed (*fig. 5*), so that the latter is consequently intranuclear.

It is very interesting to compare this stage with the previous one (*fig. 4*), taking into consideration the kinoplasmic centers, the shape

of the nuclear cavity, and the spindle. As regards the centers of kinoplasmic activity, in the preceding stage the kinoplasm is shown in the process of accumulation at the two poles, and a single clearly differentiated granule may be interpreted as the first visible indication of approaching spindle formation. At the time when the equatorial plate is formed, the kinoplasmic material becomes massed more densely than before, and two very large centrosphere-like structures are differentiated at the poles of the spindle (*figs. 5, 6*). These kinoplasmic bodies have a compact, well-defined form, but are without radiation. The nuclear cavity at the stage of metaphase is smaller than before, and the poles of the spindle become drawn closer together. The development of the spindle proved very difficult to study, and its history is discussed later in the paper under the head of spindle formation.

The accumulations of kinoplasm at the poles of the spindle are very characteristic and resemble the centrospheres described by DAVIS (**18**) in the tetraspore mother cell of Corallina, except that the latter have well-defined radiations. The chromosomes when arranged in the equatorial plate are readily counted if viewed in transverse sections of the spindle (*fig. 7*), as well as during prophase (*figs. 3a, 3b*), and the number is clearly 20. Granular fragments of the nucleolus are always present in the nuclear cavity during the metaphase, after which they disappear.

The duration of metaphase is rather long and the centrosphere-like structures persist until late anaphase. When each group of daughter chromosomes passes to the pole of the spindle, there are left only a few fibrils forming a central spindle between them (*fig. 8*). After anaphase the kinoplasm intrudes into the nuclear cavity and the central spindle gradually disappears (*fig. 9*). The kinoplasm thus surrounds the groups of daughter chromosomes, and the centrosphere-like structure loses its distinct differentiation and becomes a cloudy mass of kinoplasm without a clearly defined boundary (*fig. 9*).

Each group of daughter chromosomes, which during anaphase had a flattened form, becomes more or less spherical, with a small space within (*fig. 10*). The mass of chromosomes surrounded by granular kinoplasm comes to lie in nuclear sap or caryolymph, and

it seems possible that the nuclear membrane may be formed as the result of the contact of the caryolymph with the surrounding cytoplasm (*fig. 11*). Such conclusions were drawn by LAWSON (**44**) and GRÉGOIRE and WYGAERTS (**36**) in their studies of the telophase of mitosis. The chromosomes later lose their individual outlines and the mass becomes transformed into a chromatin network (*fig. 12*). A new nucleolus is then formed in the daughter nucleus.

No mention has yet been made of the manner of cell division. The coarse alveolar structure of the cytoplasm taken as a whole persists during mitosis, the kinoplasm associated with the division of the nucleus remaining distinct from the alveolar cytoplasm and reacting more deeply to the plasma stains. The daughter nuclei when formed lie above one another in the germinating tetraspore. Before they have attained their full size a cleavage furrow appears at the middle region of the cell which is at first very shallow. The central spindle that lay between the two groups of daughter chromosomes has entirely disappeared before the cleavage furrow is formed, so that the center of the cell is filled by cytoplasm which presents a very coarse alveolar structure, especially in the middle region, where the cleavage furrow begins (*fig. 13*). This furrow proceeds inward, the only visible assistance in its development being the extensive fusion of vacuoles by the breaking of their limiting membranes so that less resistance is presented to its progress. Finally, the furrow reaches nearly to the center of the cell (*fig. 14*), so that the tetraspore becomes divided into daughter cells, which are in communication by a strand of protoplasm, as is so generally characteristic of the red algae.

THE FIRST MITOSIS IN THE GERMINATING CARPOSPORE.

The carpospore on its escape from the cystocarp is somewhat pear-shaped, but it gradually assumes an oblong or spherical form while floating in the water. The coarse alveolar structure of the cytoplasm, the arrangement of the plastids, and the fine linin network within the nucleus (*fig. 15*) are similar to those of the tetraspore. Moreover, the first mitosis takes place at about the same period after their escape from parent plants, namely after about fifteen hours.

The history of the mitosis in the germinating carpospore is so

similar to that in the tetraspore that it seems best to point out only the marked differences between the two. The delicate linin network within the nucleus passes into a coarse chromatin reticulum upon which chains of chromatin granules appear here and there (*figs. 16a–16c*), and these are prochromosomes, as illustrated in the preceding figures of the tetraspore (*figs. 2a–2c*). The number of prochromosomes, however, is 40, and consequently double the number in the germinating tetraspore. The 40 prochromosomes grow more and more homogeneous in structure and finally become elongated chromosomes (*figs. 17a, 17b*). The weakly staining linin network disappears, but short threads remain attached at the ends of chromosomes. The kinoplasm surrounding the nuclear membrane becomes accumulated at the two poles of the nucleus, where a centrosome-like body may always be found (*fig. 18a*), and this accumulation of kinoplasm proceeds still further until there are two conspicuous centrosphere-like structures differentiated at metaphase (*fig. 19*). The spindle is somewhat larger and broader than that in the tetraspore, because of the double number of chromosomes (*fig. 19*). The polar view of that stage (*fig. 20*) clearly shows the number 40.

The nucleolus fragments during metaphase, the portions lying beside the spindle (*fig. 19*) and sometimes remaining until anaphase, after which they disappear. The behavior of the daughter chromosomes after anaphase is the same as during mitosis in the tetraspore; the groups of daughter chromosomes gather at the poles of the spindle (*fig. 21*) and become surrounded by granular kinoplasm (*fig. 22*). At the time of the formation of the nuclear membrane, the chromosomes may still be recognized and estimated as 40 (*figs. 23a, 23b*). The daughter nuclei increase in size by the secretion of nuclear sap (*figs. 24a–24c*), and finally the chromatin becomes distributed over a linin network in the resting nucleus (*fig. 25*). The germinating carpospore becomes divided by a cleavage furrow in a similar manner to that of the tetraspore.

The second and third mitosis in both germinating tetraspore and carpospore were also studied, and they were similar to those of the first divisions, showing always the two essential differences in the number of chromosomes.

MITOSIS IN THE VEGETATIVE CELLS OF THE MALE, FEMALE, AND TETRASPORIC PLANTS.

To make sure of the number of chromosomes contained within the nuclei throughout the life history, the mitoses in vegetative cells of the three forms of Polysiphonia plants—male, female, and tetrasporic—were studied. The following is a very brief account of the essential features of these mitoses.

The nuclei in the apical cells of any of the three forms of plants are somewhat larger in size than those in older region of the thallus; but although it is not difficult to obtain the successive stages of mitosis in older parts, the nucleus of the apical cell is somewhat more favorable for study and will be used in this description.

The cytoplasm in the apical cell shows very fine alveolar structure, the plastids lie near the wall, and the nucleus in the resting stage resembles that in the germinating carpospore and tetraspore (*figs. 26, 45*). The linin network becomes coarser (*figs. 27, 46*), and finally in the case of the male (*figs. 28, 29*) and female plants (*fig. 36*) 20 chromosomes appear, whereas in the tetrasporic plant (*fig. 47*) 40 chromosomes are present. The chromosomes may be readily counted at metaphase in polar views of equatorial plates, when it is evident that the sexual plants have 20 (*figs. 31, 38*) and the tetrasporic plants 40 (*fig. 50*). In spite of the small size of the nuclei, kinoplasmic accumulations at opposite poles of the nucleus are evident during prophase, and deeply staining centrosome-like bodies are conspicuous at the poles just before the spindle is formed (*figs. 29, 36*). Centrosphere-like structures are very conspicuous at the poles of the spindle during metaphase (*figs. 30, 37, 48*). These structures are more clearly shown in the mitosis in older regions of the thallus. *Fig. 43* illustrates such a mitosis from a female plant, those of the male and tetrasporic plants being omitted to avoid repetition. The smaller size of the nuclear cavity during metaphase is as constant a character of these mitoses as of those in the tetraspores and carpospores. After metaphase the two sets of daughter chromosomes remain included in the old nuclear membrane for a while (*figs. 32, 39, 49*). During the anaphase the groups become further separated, the nuclear membrane disappears, and a large vacuole intrudes between them (*figs. 33, 41, 51*). When the daughter nuclei are completely formed, a cleavage furrow develops at the periphery in the middle region of

the cell (*figs. 35, 42*), a large vacuole being present in the center. The mechanism of constriction by the cleavage furrow is probably greatly assisted by the presence of this single vacuole, in place of numbers of smaller ones which are found in the tetraspores and carpospores.

SPERMATOGENESIS.

The sperms or spermatia are formed normally on special short branches called antheridia, which are developed in clusters at the tips of the main filaments. The antheridium consists of an axial siphon (*diagram 1*) which becomes surrounded and covered by a large number of small cells. These generally develop sperm mother cells at the periphery of the antheridium, and may consequently be called "stalk cells." The mitoses in the axial siphon of the antheridium were studied (*fig. 52*), as well as those which form the stalk cells (*fig. 53*), and they showed the number of chromosomes to be 20. The methods of chromosome formation, the development of the intranuclear spindle, and the cell division by constriction are the same as those of the vegetative cells already described.

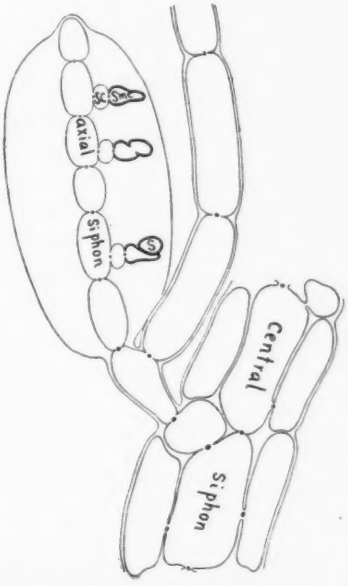


DIAGRAM 1.—Section of an antheridium, showing position of axial siphon, stalk cell (*sc*), sperm mother cell (*smc*), and development of the sperm (*s*).

The formation of the sperm mother cells from the stalk cells (*fig. 54*) is illustrated in *figs. 55–61*. *Fig. 55* presents the prophase of of the mitosis, *fig. 56* metaphase, *fig. 57* the equatorial plate viewed from a pole, *fig. 58* shows anaphase, and *figs. 59* and *60* illustrate telophase. The cell division by constriction is shown in *fig. 61*. The sperm mother cell (*fig. 62*) increases in size and assumes its characteristic form, which is narrow at the periphery and swollen at the base. In rare cases the formation of the stalk cell is omitted,

so that sperm mother cells are developed directly from the axial siphon of the antheridium.

The cytoplasm of the sperm mother cell (*fig. 62*) has a very delicate granular structure and is generally destitute of plastids. The nucleus in the resting state contains a fine network and a nucleolus. Prochromosomes, 20 in number, are formed in the network (*figs. 63, 63a*) and are connected by weakly staining linin threads. The prochromosomes increase in size and become rod-shaped chromosomes (*figs. 64, 64a*).

Kinoplasm becomes differentiated from the surrounding cytoplasm and accumulates at the poles of the elongating nucleus, and a centrosome-like body appears at each pole (*figs. 64, 64a*). The stage of prophase passes into metaphase (*figs. 65, 65a*), when centrosphere-like structures are well-developed and the axis of the spindle is shorter than the diameter of the equatorial plate, as is the case during the mitoses within the carpospores, tetraspores, and vegetative cells. The number of chromosomes is clearly 20 in this mitosis, as shown in polar view of the equatorial plate (*fig. 66*). The nuclear membrane is present during metaphase (*fig. 67*), and as the two groups of daughter chromosomes separate a vacuole intrudes between them (*figs. 68, 69, 70*). The centrosphere-like structures are not recognizable after metaphase. The set of daughter chromosomes which passes to the basal region of the cell becomes aggregated, surrounded by a nuclear membrane, and enters into a resting condition; while the chromosomes of the other set, passing to the upper part of the cell still retain their individuality, although it is probable that a very delicate membrane may be formed (*fig. 70*).

A cleavage furrow in the middle region of the cells appears (*fig. 71*), and by the same mechanism as in the case of vegetative cells effects a separation of the upper half as a sperm cell from the lower half. The greater part of the large vacuole is included in the sperm, which consequently has a relatively small amount of protoplasm in comparison with its size (*figs. 72, 73*). The cleavage furrow which cuts off the sperm cell crosses the sperm mother cell obliquely, and consequently the sperm assumes a lateral position, allowing the sperm mother cell to elongate. When the matured sperm is detached completely from the sperm mother cell, the latter has assumed again its characteristic extended form (*fig. 75*).

The sperm when detached is oval in form (*fig. 73*), and has a thin wall derived from the mother cell, and a large vacuole occupies almost all the cell cavity. The cytoplasm is therefore forced to lie in a thin layer under the cell wall, and the nucleus occupies the larger end of the oval. The chromosomes maintain their individuality and are connected with one another by delicate linin threads (*figs. 74, 74a*).

The nucleus remaining in the sperm mother cell after the formation of the first sperm divides at once, passing through prophase (*fig. 75*), metaphase (*figs. 76, 78*), and anaphase stages (*figs. 79, 80*), following the same history as in the previous mitoses. Here is apparent also the same conspicuous difference in the form of the nucleus between prophase and metaphase (*figs. 75, 76*), 20 chromosomes (*fig. 77*) always appearing in this critical stage. Finally, the telophase of mitosis is followed by cell division through a cleavage furrow, which cuts off the second sperm (*fig. 81*) in a similar manner to the first. The nucleus which remains in the sperm mother cell may repeat the process, forming a third sperm.

The successive formation of sperms by constriction from the sperm mother cell may be compared, in a general way at least, to the process of formation of conidia in certain groups of fungi, where the conidia are developed successively by constriction from a conidiophore. Of course such a comparison is a superficial one, since conidia are by no means comparable to sperms in the phylogenetic sense. The spermatia found in the rusts and lichens, and certain antheridia of the Laboulbeniaceae present greater resemblances. THAXTER (**78**) describes an exogenous method of sperm formation in Ceratomyces and Zodiomyces, in which sperms are developed successively from a definite point at the distal end of fertile cells of the antheridial branches, agreeing thus with the process in Polysiphonia.

WOLFE (**86**) considers the sperm of Nemalion to be the homologue of an antheridium because the sperm nucleus divides into two. No mitosis was found in the sperm of Polysiphonia, although this matter received careful attention. The sperm of Nemalion also escapes as a naked or thin-walled protoplast from the parent cell-membrane, while that of Polysiphonia becomes detached and retains the parent cell wall. The differences, however, do not seem to the author to affect the relationship of these two sperms as homologous structures. That of Polysiphonia is also the homologue of a uni-

cellular antheridium, in which mitosis, if ever present, has been suppressed, and the cell as a unit has become the male sexual element.

FORMATION OF THE PROCARP.

Development of the carpogonial branch.—The female organ or procarp consists in the beginning of a short branch of three or four cells. The most important of these is a cell of the axial siphon which lies next to the apical cell (*diagram 2, A*). This cell increases in size more rapidly than do the adjacent cells of the filament, so that it is very easy to recognize the primordium of the female organ, and divides successively to form five peripheral cells, which finally com-

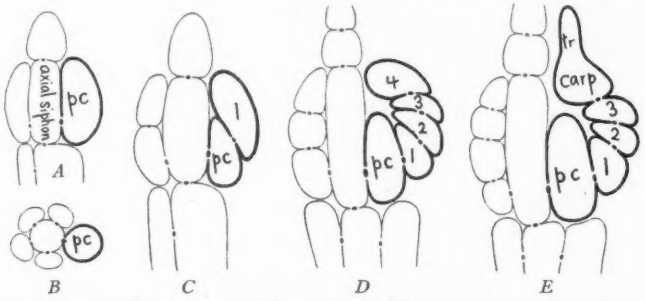


DIAGRAM 2.—Development of the carpogonial branch: *A*, young procarp with pericentral cell (*pc*); *B*, cross section of *A*; *C*, formation of first cell of carpogonial branch; *D*, the four cells of carpogonial branch; *E*, development of trichogyne (*tr*) from fourth cell or carpogonium (*carp*) of the carpogonial branch.

pletely surround it (*diagram 2, B*). The first stage is illustrated in *figs. 82–84* and the second in *figs. 85–87*. The third and fourth divisions of the siphon cell have not been figured, but they occur in such a manner that the third and fourth peripheral cells are formed opposite each other and between the first and second (*diagram 2, B*). The fifth division gives rise to a peripheral cell between the first and the fourth, which later develops the carpogonial branch and has been called the pericentral cell.

During every nuclear division concerned with the formation of the peripheral cells, 20 chromosomes constantly appear, as shown in polar views (*figs. 83, 86*), and this number is passed over to the pericentral cell. The nucleus in the pericentral cell divides in a direction nearly parallel to the axis of the procarp (*figs. 89–93*), cutting off a cell which develops the carpogonial branch (*diagram 2, C*). The

pericentral cell later also gives rise to a group of auxiliary cells. The carpogonial branch consists of four cells which are formed successively as shown in *diagram 2, D, E.* It is somewhat bent, so that the terminal cell lies almost above the pericentral cell. This terminal cell becomes the carpogonium and develops the trichogyne. The mitoses concerned with the development of the carpogonial branch are illustrated in *figs. 94–99,* and invariably showed 20 chromosomes at metaphase. As the result of these successive mitoses, the carpogonial branch extends at one side of the central axial cell, with the pericentral cell situated between them (*diagram 2, E*).

The nucleus in the fourth or terminal cell of the carpogonial branch divides (*fig. 100*) to form two nuclei (*fig. 101*), each with 20 chromosomes, one of which becomes the female gamete nucleus, while the other enters the trichogyne that is formed at once. The upper end of the cell pushes out as a delicate process which contains almost from the beginning one of the two nuclei, the other remaining in the basal swollen region of the cell called the carpogonium (*figs. 102, 103, 104*), which corresponds to an oogonium. The formation of the trichogyne completes the development of the female organ, whose parts in longitudinal section are shown in *fig. 103.*

The trichogyne.—The trichogyne nucleus, as a rule, is situated in the middle region of the trichogyne, which has about the same breadth throughout its tubular cavity, but becomes constricted below where it joins the carpogonium. No plastids could be found in the trichogyne.

The presence of a trichogyne nucleus in the red algae has been a subject of some controversy. SCHMITZ (**69**) described a large single or several small granular bodies, which stained like chromatin, in the trichogyne of *Batrachospermum moniliforme* and Gloeosiphonia before fertilization, but he gives no interpretation further than the few words, "Derivate des Zellkerns der weiblichen Zellen?" Eight years later DAVIS (**17**) observed in the same species of Batrachospermum an unmistakable nucleus in the trichogyne, staining with haematoxylin as a dark blue body. OLTMANNS (**55**) also observed the granule within the trichogyne of Gloeosiphonia, but he regarded it as having no connection with the nucleus. SCHMIDLE (**68**) failed to find the nucleus in the trichogyne of Batrachospermum, and OSTERHOUT (**57**) contends that it is not present. WOLFE (**86**)

observed a nucleus in the trichogyne of Nemalion, which he assumes to be derived from the young carpogonium, although the mitotic figure was not found. The presence of a nucleus in the trichogyne necessitates a modification of our conception of the morphology of the female organ in the red algae.

The earlier conception of the morphology of the trichogyne as given by SCHMITZ (**69**) was a cytoplasmic extension of the carpogonium, developed as the receptive organ for the sperm. This conception was followed by OLTMANNS (**55**), SCHMIDLE (**68**), and OSTERHOUT (**57**). DAVIS (**17**), however, concluded that the trichogyne is not a cytoplasmic extension from the carpogonium, but that it possesses a well-defined nucleus and hence has a certain degree of independence. The trichogyne of Batrachospermum has certainly a body that must be regarded as a chromatophore. WOLFE'S studies of Nemalion (**86**) support this view with respect to a trichogyne nucleus. In Polysiphonia, as stated above, there is present a trichogyne nucleus whose origin has been traced to a division in the terminal cell of the carpogonial branch. These facts have an important bearing on the structure of the trichogyne in lichens and Laboulbeniaceae. THAXTER (**78**) has described multicellular branching trichogynes in certain forms of Laboulbeniaceae, and the long multicellular trichogyne of Collema (BAUER **6**) and Physcia (DARBISHIRE **16***a*) illustrate similar conditions. In the lower forms of algae where heterogamy is established, male and female gametes are generally formed in unicellular antheridia and oogonia. The female gametes having become non-motile, usually remain within the oogonium and are fertilized by motile male gametes which enter the oogonium through a pore, as is illustrated by Oedogonium. With the loss of motility on the part of the male gametes, a receptive region or structure seems to have been developed by the oogonium, and in this manner the trichogyne probably arose. However, the development of the trichogyne means that the female cell, which is the homologue of an oogonium, acts as a unit. Should there be in such a cell one or more mitoses, which are the remnants of ancient nuclear division when two or more gametes may have been developed, then the supernumerary nuclei would be expected to degenerate. This seems to be the condition in the red algae, where there is an extra nucleus beside the one

which is in the gamete. This extra nucleus has an important relation to the development of the trichogyne, which consequently is much more than a mere cytoplasmic extension from the carpogonium; for having a nucleus it may possess the possibilities of a somewhat extensive development. This is perhaps the explanation of the multicellular trichogynes of the lichens and the Laboulbeniaceae, which in some forms of the latter group are extensively branched.

The passage of the sperm nucleus through the trichogyne into the carpogonium.—The nucleus of the carpogonium increases in size as the female cell matures, while the nucleus of the trichogyne remains about the same size as when it was formed (*fig. 104*). The sperm becomes attached to the tip of trichogyne (*fig. 105*). The walls between the two structures dissolve, and the contents of the sperm flows into the trichogyne (*fig. 106*). The sperm nucleus consists of a number of deeply staining bodies (about 20), which are chromosomes. The nuclear membrane if present must be very delicate, for it could not be positively recognized (*figs. 106–108*). The deeply staining sperm nucleus in the trichogyne is in sharp contrast with the smaller trichogyne nucleus whose chromatin content stains weakly. The sperm nucleus moves downward, passing the trichogyne nucleus (*figs. 107, 108*), and enters the carpogonium. The female nucleus in the carpogonium, which until this time lay at the bottom of the cell, seems to move upward a short distance as if to meet the sperm nucleus (*fig. 109a*). The two gamete nuclei are strikingly dissimilar at the time of union, the male consisting of a densely packed aggregation of chromosomes, while the female is larger and in a typical resting condition, with chromatin distributed over a linin network (*fig. 109a*).

The trichogyne nucleus may still be recognized after the sperm nucleus has passed into the carpogonium. However, the cytoplasm of the trichogyne soon shows signs of disorganization, first at the tip, and a little later the trichogyne nucleus breaks down. When the male nucleus is in contact with the female and becomes somewhat pressed against it, the cytoplasm of the trichogyne has probably always separated from the carpogonium and the trichogyne has begun to shrivel.

Formation of the auxiliary cells.—Parallel with the fusion of the gamete nuclei there takes place the development of a set of auxiliary

cells, as shown in *diagram 3*. The pericentral cell, which was the progenitor of the carpogonial branch and lies beneath the carpogonium (because of the growth and bending of this structure), now gives rise to two cells (*diagram 3, a1, a'1*), one somewhat below and the other at the side. The cell below divides once (*diagram 3, a'1, a'2*). The cell at the side develops a branching group which lies close beside the carpogonial branch, as shown in *diagram 3* (*a 1, a 2, a 2', a 3, a 3'*). One of these auxiliary cells (*a 3*) is formed between the fertilized carpogonium and the pericentral cell. Thus the final result is two series of auxiliary cells, one consisting of five, the other of two cells; and in the former series it should be remembered that one of them has an important function, as will appear later, becoming the path of communication between the fertilized carpogonium and the pericentral cell.

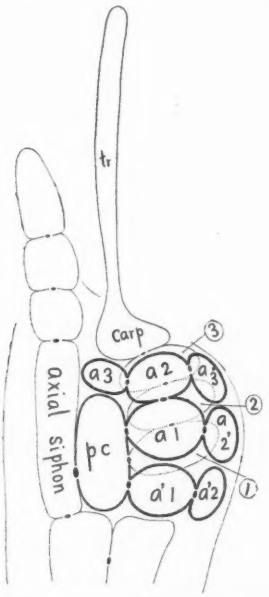


DIAGRAM 3.—Mature procarp showing arrangement of auxiliary cells: *pc*, pericentral cell; *a1*, *a2*, *a2'*, *a3*, *a3'*, *a'1*, *a'2*, auxiliary cells; 1, 2, 3, cells of carpogonial branch; *carp*, carpogonium; *tr*, trichogyne.

PHILLIPS (**60**) in his studies on the Rhodomelaceae recognized many features in the structure of the procarp of Polysiphonia which I have just described. His account of a four-celled carpogonial branch is correct, together with the general account of the formation of the central cell, as will be described presently. However, I was not able to find the arrangement of the auxiliary cells as he has described them, and his investigation lacks the cytological details through which the nuclei that enter the carpospore must be traced.

FERTILIZATION AND DEVELOPMENT OF THE CYSTOCARP.

The fusion of the gamete nuclei.—The male and female gamete nuclei which met in the carpogonium have generally fused by the time

the auxiliary cells are formed. The membrane of the female nucleus appears to dissolve at its point of contact with the sperm nucleus, which lies closely pressed against it (*fig. 114a*), and later the chromatin content of the male nucleus enters the female (*fig. 115a*). The subsequent changes in the female nucleus result in the gradual transformation of its linin network into clearly defined chromatin granules and finally into chromosomes. At the same time the crowded group of male chromosomes (*fig. 115a*) becomes looser, the chromosomes separating from one another, some remaining near the periphery of the fusion nucleus, and some passing into the interior. Finally the chromosomes derived from male and female nuclei become mingled together and the fusion nucleus assumes the appearance of prophase (*fig. 116*).

The first mitosis of the fusion nucleus (sporophytic).—The fusion nucleus which results from the union of the male and female gamete nuclei now passes into the prophase of mitosis. The number of chromosomes is 40, which is of course double the number in the sexual plants or gametophytes, so that the fusion nucleus is sporophytic in character. These chromosomes differ from one another in size, and some of the smaller certainly come from the male nucleus. It would be interesting to trace carefully the history and behavior of these chromosomes, but I am not prepared at present to discuss this matter in detail.

The stages of prophase in Polysiphonia, as previously described, are always characterized by the presence of centrosphere-like structures at the poles; however, these structures do not seem to be present during the first mitosis of the fusion nucleus. The spindle of this mitosis is remarkable for its size and the breadth of the poles (*fig. 117a*). Another peculiarity is the fact that the nuclear membrane disappears during prophase, so that the spindle lies freely in the cytoplasm. It is possible that the early dissolution of the membrane is connected with the fusion of the gamete nuclei, which may weaken the membrane of the female nucleus. As regards the count of chromosomes, their number 40 is apparent when the equatorial plate is viewed from the pole (*fig. 118a*). In the late metaphase the same number may be estimated in both groups of daughter chromosomes (*fig. 123*), which means that this first division of the fusion nucleus is a typical

mitosis. At anaphase there is present a rather conspicuous central spindle between the two sets of daughter chromosomes (*fig. 124a*).

The migration of sporophytic nuclei into the pericentral cell.—There is only one mitosis within the fertilized carpogonium. The carpogonium now fuses with the auxiliary cell, which lies between it and the pericentral cell (*diagram 3, a3*). The wall between these cells dissolves and a broad communication is formed connecting them. A fusion between this auxiliary cell and the pericentral cell follows at once, so that the carpogonium is then in free communication with the pericentral cell by means of the auxiliary cell. Sometimes this communication becomes established as early as the metaphase of the mitosis of the fusion nucleus. By means of the passage which is established by these cell unions, the two sporophytic daughter nuclei, resulting from the division of the fusion nucleus, move down into the pericentral cell (*figs. 125, 126*).

During the formation of the auxiliary cells from the pericentral cell each nucleus in the first three cells of the carpogonial branch divides (*figs. 119–122*). The daughter nuclei then lie side by side in pairs within the cells of the carpogonial branch. While the sporophytic fusion nucleus is undergoing mitosis, the protoplasmic connections between the cells of the carpogonial branch widen, and there is a movement of the cytoplasm along the branch into the carpogonium, possibly to furnish nourishment to this cell.

The communication between the carpogonium and the adjacent auxiliary cell is transient, simply furnishing a passage for the sporophytic nuclei into the pericentral cell. After their migration, the carpogonium becomes detached from the auxiliary cell and remains isolated for a while, without a nucleus, but finally breaks down with its three sister cells of the carpogonial branch.

The formation of the central cell and the development of the carpospores.—When the carpogonium becomes separated after its union with the auxiliary cell and the passage of its two sporophytic nuclei into the pericentral cell, all of the auxiliary cells become more closely united with one another. This condition takes place by the broadening of the protoplasmic communications that already exist between them. New communications are also established between neighboring auxiliary cells, so that the entire system becomes closely bound

together by broad protoplasmic strands. These protoplasmic communications make possible the movement of the nuclei in the auxiliary cells towards the pericentral cell. This general cell union finally results in the formation of a large irregular cell, the central cell, as it was called by previous investigators (PHILLIPS **60**, and others), containing a number of nuclei. Two of these nuclei, as previously stated, are sporophytic and derived from the mitosis of the fusion nucleus in the fertilized carpogonium; the other nuclei, perhaps three or four in number, are gametophytic and derived from the auxiliary cells. The two sporophytic nuclei lie in the upper part of the central cell and the gametophytic nuclei below. There are not as many gametophytic nuclei in the large fusion cell as might be expected, because some of them have already broken down and the others generally show signs of disorganization.

The two nuclei of sporophytic origin give rise to a series of mitoses (*fig. 127*), and the central cell now develops several lobes, into each of which a single sporophytic nucleus generally passes (*fig. 128*). The nucleus contained within each lobe divides once more (*figs. 129, 130*) and a carpospore is cut off terminally (*fig. 131*) from the lobe by a cleavage furrow, the lower portion remaining as a stalk cell by which the carpospore is attached to the central cell (*fig. 132*).

The chromosomes appearing in the mitoses previous to the formation of the carpospore are clearly 40 in number. There is therefore no chromosome reduction at this period in the life history of Polysiphonia, for the sporophytic number 40 enters the carpospore and, as previously described, appears with the first mitosis at its germination. The period of chromosome reduction in Polysiphonia is at the time of tetraspore formation, as will be discussed presently. This is an important matter in relation to WOLFE'S (**86**) account of Nemalion, where he reports chromosome reduction as taking place just before the formation of the carpospores.

After the formation of the carpospores the central cell increases greatly in size, absorbing the stalk cells (*fig. 133*); and finally the cell of the axial siphon becomes involved in these extensive cell unions, which are probably concerned with the nourishment of the carpospores, since sixty or more, as a rule, are developed in a single cystocarp. While the carpospores are being formed, the characteristic envelop

of the cystocarp becomes swollen and urn-shaped. This envelop is developed from the peripheral siphons of the procarpic branch; but is lined with a set of delicate filaments (*fig. 132, p f*), called paranematal filaments, that arise from the cell of the axial siphon.

Some of the gametophytic nuclei derived from the auxiliary cells break down before the unions or after the formation of the central cell. They swell greatly, the chromatin network becomes inconspicuous, the membrane grows thinner and finally dissolves, so that the nuclear contents mingle with the cytoplasm. Or, before the dissolution of the nuclear membrane, the network fades away, but large nucleolus-like globules appear, which after the breaking down of the membrane become distributed in the cytoplasm (*fig. 134*).

TETRASPORE FORMATION.

It is probable that true tetraspores are never formed on the sexual plants of Polysiphonia. Certain abnormalities will be discussed in the next section of this paper. The cell lineage of the tetraspore in the Rhodomelaceae was correctly described by FALKENBERG (**27**). HEYDRICH (**41, 42**) gives an account in which he contends that the tetraspores are formed after a nuclear union within the mother cell, and that tetraspore formation may be the forerunner of a method of sexual reproduction. His studies seem to have been made upon unsatisfactory material and without cytological methods, to judge from his figures. Since I have not been able to confirm his conclusions or to establish any relation between them and my own, I shall not discuss them further.

The beginning of tetraspore formation is the development of a pericentral cell laterally from the central siphon (*fig. 140, pc*). The mitosis previous to the formation of the pericentral cell (*figs. 136–139*) shows that its nucleus contains 40 chromosomes. The pericentral cell then cuts off a cell above (*fig. 140, tmc*), which becomes the tetraspore mother cell, attached by a stalk (*fig. 140, sc*) to the central siphon.

The formation of the tetraspore mother cell was traced in detail through the prophase, metaphase, and anaphase of the nuclear division in the pericentral cell (*figs. 141–146*), and the number of chromosomes which enter the tetraspore mother cell is clearly 40.

Centrosphere-like structures also appear unmistakably at the metaphase of this mitosis (*fig. 142*), as well as in the previous mitosis (*fig. 137*).

The tetraspore mother cell (*fig. 147*) increases rapidly in size, soon becoming very much larger than the stalk cell. With the growth of the cell the nucleus also increases in size, and in the resting condition shows a conspicuous linin network. This network consists at first of lightly staining anastomosing threads, having knots here and there which stain a little darker (*figs. 147, 147a*). The cytoplasm presents a fine granular structure, with small alveoli. The nuclear network undergoes gradual change in such a manner that the lightly staining threads become somewhat thicker, and the knots grow into large irregular masses (*figs. 148, 148a*). Some portions of the threads connecting the knots become thinner and more slender, at last fading away; while other portions of them become thicker, and then the knots gradually diminish in bulk; so that, by and by, the anastomosing chromatin network becomes transformed into long continuous threads of irregular thickness, finally broadening into ribbons (*figs. 149, 149a*).

These chromatin threads or ribbons derived from the network now spread and become distributed throughout the nuclear cavity in a continuous and tangled fashion, presenting no free ends. It is difficult to decide whether there is a single continuous thread or a double structure, but probably the latter condition is present, for the threads generally run side by side in pairs (*figs. 150, 150a*). Most of the chromatin threads become more tangled, twisted, and massed at one side of the nuclear cavity, only a few traversing the cavity to the opposite side of the nuclear membrane. Synapsis is now generally believed not to be an artifact, and a careful study of this stage in Polysiphonia convinces me that the uniform chromatin threads which run parallel in pairs actually fuse into a single thread in certain portions, although at the same time they may be separated in other parts. All of this probably means that the two continuous threads resulting from the transformation of the chromatin network are of distinct origin, paternal and maternal, and that they come in contact where they run closely parallel, and finally fuse together in the tangled and contracted condition of synapsis, according to the recent interpretation

of ALLEN (**1**, **2**, **3**, **4**), GRÉGOIRE (**35**), BERGHS (**7**, **8**, **9**, **10**), ROSENBERG (**64**, **65**, **66**), and others.

The period of synapsis lasts for some time, after which the spirem becomes looser and distributed throughout the nuclear cavity. This thread, at first uniform in thickness, begins to split longitudinally (*figs. 152, 152a*), the two parts lying close together side by side for long distances, but sometimes diverging at wide angles and then coming together again. The transverse segmentation of this double spirem to form the chromosomes now takes place, although not simultaneously throughout the entire nucleus. The shape of these chromosome segments is very irregular when first formed. They may be bent or twisted like two Vs (*fig. 153a, V*), or two Ls (*fig. 153a, L*) placed one above the other, or crossing in the form of an X (*fig. 153a, X*). The segments gradually shorten (*fig. 154*) until 20 short rod-shaped chromosomes, bivalent in nature, are formed (*fig. 155*). These are of course really the 40 sporophytic chromosomes now grouped in pairs. The nucleolus present in the resting nucleus of the tetraspore mother cell has not changed visibly up to this prophase stage, taking various positions, and during synapsis being surrounded by the tangled mass of threads. Thus the 40 chromosomes which entered the tetraspore mother cell now appear after synapsis, which is generally believed to be the period of chromosome reduction, as 20 pairs. These pairs become arranged in an equatorial plate and the chromosomes of the pairs split longitudinally, so that a large number of chromosomes results (*fig. 156*), probably 80 in all, but so crowded that it is not possible to count them with absolute certainty.

While these changes are taking place inside of the nucleus the kinoplasm accumulates in two opposite poles outside of the nuclear membrane. Each pole of the spindle which is formed (*fig. 156*) is occupied by a deeply staining centrosome-like body, as in the case of the prophase of the other mitoses previously described. The form of this spindle in the tetraspore mother cell is quite different from other mitoses. Its longest axis runs from pole to pole instead of across the equatorial plate, as in the other nuclear figures. Besides, the two poles are less than 180° apart, which gives an asymmetrical or somewhat bent form to the spindle when viewed from a certain

direction, and also there are no clearly defined centrosphere-like structures.

The spindle of the first mitosis is of very short duration. As soon as the chromosomes at the equatorial plate separate into two groups, the two spindles of the second mitosis suddenly appear and the first spindle can no longer be recognized (*fig. 157*). It is possible that the two poles of the first spindle may move along the membrane and become poles of the second spindle, but I have no evidence to support this suggestion. Whatever the origin of the poles of the second mitosis, they are placed in an entirely different position from the poles of the first. The second mitosis in the tetraspore mother cell, therefore, follows so shortly after the first that there is no period between for the organization of two resting nuclei.

The rapidity with which the second mitosis follows the first may prevent the organization of centrosphere-like structures at the poles. The axis of the two spindles of the second mitosis lie perpendicular to each other (*figs. 157, 158*), and the two nuclear divisions take place simultaneously. At anaphase four groups of chromosomes, 20 in number, pass to the poles, still included in the membrane of original tetraspore mother cell, which persists from the beginning (*fig. 159*). These four groups, of 20 chromosomes each, contain all together the 80 granddaughter chromosomes shown in *fig. 156*. When the granddaughter chromosomes reach the four poles of the two spindles of the second mitosis, four masses of kinoplasm are present. The granddaughter chromosomes after reaching the poles soon begin to lose their individual outline, and become connected with one another to form a network (*fig. 160*). The original nuclear cavity contains at this stage a very large nucleolus-like body which appears during the anaphase of the second mitosis (*fig. 159*). The history of this body is not clear, but it seems to be a new structure, developing during the second mitosis, The four poles now begin to enlarge, while the region of the nuclear membrane between them becomes flattened (*fig. 160*); consequently the outline of the original nuclear membrane is somewhat tetrahedral at this stage. The transformation of the four groups of chromosomes into four chromatin nets proceeds until a chromatin reticulum occupies each of the four lobes of the original nuclear cavity.

The cytoplasm of the tetraspore mother cell has large alveoli, which pass into a finer structure at the periphery of the cell and at the nuclear membrane. This fine alveolar cytoplasm around the nucleus joins the kinoplasm, which lies directly against the nuclear membrane, at the four regions formerly occupied by the poles of the spindles of the second mitosis (*fig. 160*). These kinoplasmic masses extend along the membrane between the four lobes. Finally the membrane breaks down between the lobes and the kinoplasm enters the nuclear cavity in the form of fibrils (*fig. 161*), which grow slowly towards the center, where they finally meet around the nucleolus-like body which now shows signs of fragmentation. The four groups of daughter chromosomes, passing into a chromatin network, thus become surrounded by kinoplasm (*fig. 162*) and separated from one another as four daughter nuclei (*figs. 163, 163a*). During this process the nuceolus-like body, formerly occupying the center of the nuclear cavity, fragments into four or more portions, which become distributed to the four daughter nuclei.

The daughter nuclei and the tetraspore mother cell continue their growth after nuclear division, these four nuclei remaining closely associated with one another for a long while (*fig. 165*). Cleavage furrows have begun to form at the periphery of the cell a little before or after the end of nuclear division. The arrangement of these furrows may be compared to the six edges of four spherical tetrahedrons whose apices are pointed towards the center of the tetraspore mother cell. The cleavage furrows slowly grow inward (*figs. 165, 165a*), and finally meet at the center of the mother cell between the four daughter nuclei, thus dividing the protoplast into tetraspores. The mechanism of the cell division by cleavage furrows is similar to that of the vegetative cells, *i. e.*, the furrow is assisted in its growth inward by the fusion of the small vacuoles.

Throughout the whole process of tetraspore formation the mother cell remains connected with the stalk cell by a strand of protoplasm, and probably obtains nourishment through this strand, since the developing tetraspores increase greatly in size.

ABNORMALITIES.

Normally the male and female organs and tetraspores are found on three different individuals, but it often happens that antheridia and

procarps are produced by the same plant. Sperms are occasionally developed in clusters at the nodal regions of older portions of filaments, more often on male plants, but sometimes they are formed near the base of cystocarps. The sexual cells in these cases develop normally, the successive mitoses showing 20 chromosomes.

Frequently certain of the stalk cells in an antheridium increase greatly in size (*fig. 166*) and divide again and again (*fig. 167*). The cytoplasmic structure and behavior of the cells resemble somewhat the auxiliary cells of the procarp, and it seems possible that there is present in such cases an organ of somewhat mixed character.

The most noteworthy abnormalities, however, are those where cystocarpic or antheridial plants produce cells whose lineage is identical with that of the tetraspore mother cell (*figs. 168–170g*). The development of these cells was traced until they reached their full size (*figs. 170a–170g*), yet the nuclei in almost all cases remained undivided (*fig. 170d'*), although the beginnings of cleavage furrows were observed as shallow grooves (*figs. 169–170g*). These cleavage furrows never proceeded to the interior of the cell. Very rarely the nucleus appeared to enter a mitosis (*figs. 171, 171a, 171a'*) in old cells, but the number of chromosomes, small and round, were about 20 in each daughter group, and there was no evidence of reduction phenomena; indeed, the cell was never divided. Whether this cell may escape from the parent plant and germinate as a monospore has not yet been determined.

It seems probable that this peculiar behavior in Polysiphonia may offer an explanation of similar cases reported in the red algae where tetraspores are formed on sexual plants. They have been noted in *Chylocladia kaliformis* (Lotsy **45**), *Spermothamnion Turneri* and *Ceramium rubrum* (Davis **24**), and Davis has also observed them on *Callithamnion Baileyi*. Such cases should be carefully investigated to determine whether true tetraspores are present or whether the structures are not really of the nature of monospores, as in Polysiphonia, and developed with a suppression of reduction phenomena. In this case the apparent irregularity of the presence of asexual spores on a sexual plant would be explained; or it is of course possible that in some cases the tetraspores are formed normally, but the sexual organs are developed apogamously. However, it

seems more probable that the first alternative will be found to be the explanation of these exceptional conditions in the red algae.

DISCUSSION OF CYTOLOGICAL PHENOMENA.

The nucleolus.—The morphology of the nucleolus and its behavior and function during mitoses have been studied in some detail for two decades by many investigators in both plant and animal cells. Various conclusions have been reached by different authors for the various forms examined, and the same author has not unfrequently changed his view when he came to study different material. From the excellent comparative studies of MONTGOMERY (**48**) and work done later, it is possible to summarize the essentials of the most important views as follows.

ZACHARIAS (**88**) proposed the theory that the nucleolus contains no chromatin, after FLEMMING'S conclusion (**33**) that there were chemical differences between true nucleoli and the chromatin reticulum. This view has been followed by various authors, who have concluded that there is no relation between the formation of chromosomes and the disappearance of nucleoli. This seems to be the condition in Polysiphonia.

STRASBURGER (**72**, **74**) published the view that the substance of the nucleolus is utilized for spindle formation, which conclusion was drawn from the fact that the nucleolus in many forms disappears partly or completely, immediately preceding the formation of the spindle. Later NĚMEC (**54**) suggested that the disappearance of the nucleolus and the formation of the spindle may be regarded as two independent events, which take place simultaneously. STRASBURGER'S view has been followed by FAIRCHILD (**26**), HARPER (**38**), WILLIAMS (**81**), and others. The spindle formation of Polysiphonia will be considered in the next section under the heading "spindle formation."

STRASBURGER (**70**), however, formerly held the view that the nucleolus was reserve material serving to build up the chromosomes. This theory has been followed by PFITZNER (**59**), GUIGNARD (**37**), FARMER (**29**, **30**), SARGANT (**67**), SWINGLE (**76**), CARNOY and LEBRUN (**13**), CHAMBERLAIN (**15**, **16**), DUGGAR (**25**), ANDREWS (**5**), MOTTIER (**52**), CAVARA (**14**), WAGER (**80**), and others.

Some authors have gone still further and concluded that the chromosomes in certain forms are formed directly from the nucleolus. The studies of the algae and of lower unicellular organisms seem to support this conclusion. Thus TANGL (**77**), MEUNIER (**46**), MOLL (**49**), DECAGNY (**24***a*), HENNEGUY (**40**), MITZKEWITSCH (**47**), and VAN WISSELINGH (**83**, **84**) on Spirogyra, GOLENKIN (**34**) on Sphaeroplea, and WOLFE (**86**) on Nemalion hold this view. There are naturally some differences in details among the authors mentioned above. For example, MOLL states that the nucleolus of Spirogyra is found commonly exhibiting a skein structure, and that segments are formed by the transference of chromatin substance from the nucleolus into a nuclear plasm as small fragments arranged like beads in a necklace. MITZKEWITSCH points out that during mitosis the nucleolus increases in size and becomes differentiated into a number of deeply staining granular chromosomes. VAN WISSELINGH believes that in the same genus only two out of the eight chromosomes are derived from the nucleolus, and that in the reorganization of daughter nuclei both halves of these two chromosomes give rise to the new nucleoli. GOLENKIN describes the nucleolus of Sphaeroplea as breaking up into a number of chromosomes which become arranged in a nuclear plate. WOLFE on Nemalion states that the material of the nucleolus passes outward through radiating fibrillae (linin ?) into a number of chromatin granules, which organize the chromosomes directly without the intervention of a spirem stage.

The most recent study on Spirogyra is by BERGHS (**11**). He concludes that the nuclear network is not of chromatin nature, at least it contains in the resting state little chromatin and does not take part in the formation of chromosomes, whereas the nucleolus, at least at prophase, contains all of the chromatin elements and does not disappear at any moment of mitosis. The nucleolus consists of two substances; from the first, 12 chromosomes become differentiated and arranged in a ring at the equatorial zone; the second substance remains in the form of the original nucleolus. The second substance at anaphase splits into two groups of small rods ("bâtonnets"), forming segments which pass to the poles with the chromosomes. These segments are 6 in number, but are double longitudinally. The true chromosomes become attached in pairs at the equatorial ends of these segments.

The daughter nucleoli are reconstructed at the expense of the double segments. These undergo an active vacuolization and are then condensed into a nucleolus in which the two substance are again mixed together.

According to other views, there may be more than one kind of structure called a nucleolus. CARNOY (**12***a*) makes four groups of these structures as follows: *nucléolus nucléinieus*, *nucléolus noyaux*, *nucléolus plasmatiques*, and *nucléolus mixtes*, the first one being considered as portion of the chromatin network and the third concerned with the formation of the spindle. Other authors (ROSEN **62**, DAVIS **22**, WILSON **82**) have recognized two kinds of nucleoli, true nucleoli and chromatin nucleoli, the latter being considered entirely of chromatin.

In Polysiphonia the nucleolus lies in various positions within the nuclear cavity, and is not connected with the chromatin network. The chromosomes are formed from the gradual transformation or rearrangement of the substance of the network, and the nucleolus takes no part in their development. In Corallina also DAVIS (**18**) clearly distinguishes the chromatin bodies from the nucleolus.

Spindle formation. — The spindle fibers in Polysiphonia are meagerly developed and of short duration. During the prophase of mitosis the nucleolus remains unchanged and the two poles are marked by deeply staining bodies, but I regret that I have not been able to trace the process of spindle formation. In the sporelings, where the nucleus is comparatively large in size and the spindles are more conspicuous, it was noted that short slender fibrils are attached to the chromosomes when assembled irregularly in the middle region of the nuclear cavity (*figs. 3, 17*). These fibrils are the remains of the nuclear network and are the only fibrillar structures ever seen within the nuclear membrane at this time. The centrosome-like bodies, which at metaphase seem to become the centers of the well-differentiated centrosphere-like structures, have no radiation into the cytoplasm, though in the case of sperm mother cells a few fibrillae may be seen running from the centrosome-like bodies at prophase (*fig. 64*). I have not observed the entrance of spindle fibers from the kinoplasmic centers outside of the nucleus, as has been reported by DAVIS (**18**) for Corallina.

HARPER (**39**) states that, after the synaptic stage in the ascus of Phyllactinia, a number of strands of chromatin are attached to a central body, and that each strand corresponds to a single chromosome. He shows that the resting nucleus of Phyllactinia has definite polarity. The formation of chromosomes from a strand of the spirem consists in the segregation of two substances present in the spirem. The densely staining chromatin aggregates into chromosomes, leaving the achromatic portion as a series of threads connecting the chromosomes to the central body, and these threads later form the spindle. I have studied Polysiphonia very carefully in the hope of relating its process of spindle formation to that of Phyllactinia, but have not been able to find any essential resemblance. There seems to be no polarity to the resting nucleus of Polysiphonia as described by HARPER for Phyllactinia.

Centrosome and centrosphere-like structures.—Every mitosis, no matter where it occurs, is characterized by the constant presence during prophase of two sharply differentiated centrosome-like bodies in the center of the kinoplasm at opposite ends of the nucleus. When the chromosomes are arranged in the equatorial plate the kinoplasm has the form of a large centrosphere-like structure at the pole of the spindle, and the centrosome-like bodies have disappeared. These structures are destitute of the astral rays, characteristically accompanying typical centrosomes or centrospheres, as reported in Fucus (STRASBURGER **73**, FARMER and WILLIAMS **32**), Stypocaulon (SWINGLE **76**), Dictyota (MOTTIER **52**, WILLIAMS **81**), and in animal cells. They have a compact, homogeneous structure in Polysiphonia, which makes them readily distinguishable from the surrounding protoplasm. The daughter chromosomes, after their separation at the equatorial plate, become gathered close to each centrosphere-like structure at anaphase of mitosis, and in contact with it. The latter then passes into a vague kinoplasmic mass which surrounds the group of daughter chromosomes.

The observations summarized above, namely the appearance of a centrosome-like body at prophase, its progressive development and differentiation as a large centrosphere-like structure during metaphase, which is the climax of the kinoplasmic activity of mitosis, and its gradual decline after anaphase, lead me to conclude that these

structures in Polysiphonia are not permanent organs of the cell, but are formed *de novo* with each mitosis, to carry on the mechanism of nuclear division.

HARPER (**39**) has published an important discussion on a "central body" discovered by him in Phyllactinia. In this form the central body lies within the membrane of the resting nucleus, and is connected with chromatic strands so as to give polarity to the nucleus. The poles of the spindles are formed by division of the central body. HARPER believes in the permanence of this structure, from mitosis to mitosis, and in the maintenance of its connection with the chromatin. The permanent nature of the central body in Phyllactinia and the transient appearance of centrosphere-like structures in Polysiphonia seem at present difficult of reconciliation.

In Nemalion WOLFE (**86**) reports that centrosomes are present without astral rays at metaphase, but their continuity was not established. The centrosphere described by DAVIS (**18**) in the tetraspore mother cell of Corallina is formed *de novo* in each mitosis. Their transient nature agrees with the somewhat similar structures of Polysiphonia.

The reduction of chromosomes.—STRASBURGER'S paper (**71**) entitled "The periodic reduction of the number of chromosomes in the life history of the living organisms" was the first presentation of the significance of sporogenesis and reduction phenomena in relation to alternation of generations in plants. His conclusions were based upon the discoveries that nuclei in the sporophyte generations of higher plants have double the number of chromosomes found in the nuclei of the gametophyte generations, and that the reduction of this double number takes place at the period of sporogenesis. This theory has been well established so far as groups of plants above the thallophytes are concerned, and the period of chromosome reduction has been found to be always associated with sporogenesis, and never with gametogenesis as in the case of animals. However, among the thallophytes our actual knowledge of facts concerning the reduction period is meager.

Suggestions of the presence of reduction phenomena at gametogenesis have been made among the fungi in the Peronosporales (ROSENBERG **63**) and Saprolegniales (TROW **79**). ROSENBERG

describes what he has called a synaptic stage in the nucleus preceding the two mitoses concerned with oogensis in Plasmopara, and TROW holds that chromosome reduction takes place in the two mitoses in the oogonium of Achyla. These interpretations have been discussed and criticized by DAVIS (**21**, **23**), and the suggestions of ROSENBERG and TROW do not seem to me convincing.

Among algae, one of the best known accounts of gametogenesis is that of Fucus (STRASBURGER **73**, FARMER and WILLIAMS **32**), where, although spermatogenesis has not been investigated, the history of oogenesis indicates a period of chromosome reduction. Consequently the fusion nucleus in the fertilized egg has the same number of chromosomes as the nucleus in the vegetative plants of Fucus, which led STRASBURGER (**73**, **75**) to conclude that the Fucus plant is a sporophyte generation and that the gametophyte is so greatly reduced that it is only represented by single cells —male and female gametes —before fertilization.

Other examples among the thallophytes in which the life history has been worked out in some detail are Dictyota and Nemalion. In Dictyota (WILLIAMS **81**) the fertilized egg nucleus gives rise to an asexual plant with double the number of chromosomes, and consequently a sporophytic generation. This asexual plant develops spores in groups of four accompanied by chromosome reduction, and these spores develop the gametophyte generation. This type of life history is clearly analogous to that of Polysiphonia. In Nemalion (WOLFE **86**) the fusion nucleus of the fertilized carpogonium has a double number of chromosomes which appear in all of the cells of the cystocarp (sporophytic) up to the formation of carpospores, where the reduced number of the gametophyte is reported to appear. WOLFE's account, however, does not give the details of this chromosome reduction with the characteristic stage of synapsis followed by two successive mitoses.

Chromosome reduction in Polysiphonia is clearly similar to the phenomena of sporogenesis in higher plants, and takes place at the time of tetraspore formation. The carpospores, containing the sporophytic number of chromosomes, continue the sporophyte generation by developing the tetrasporic plant. The appearance of synapsis just previous to the formation of the tetraspores, followed by two succes-

sive mitoses with their peculiar distribution of the chromosomes, is similar in all essentials to the reduction division in the higher plants and in Dictyota.

The mitoses in the tetraspore mother cell have certain peculiarities that deserve special consideration. The first mitosis is followed so rapidly by the second that there are no resting nuclei organized between the two divisions. In this respect the history of sporogenesis resembles that of Pallavicinia reported by MOORE (**50**, **51**), but there is this difference, that in Polysiphonia the granddaughter chromosomes present in the second mitosis are formed before the first and within the original membrane, and the organization of the four granddaughter nuclei takes place simultaneously. However, the distribution of the granddaughter chromosomes is clearly effected through two mitoses and two sets of spindles, so there is never present a quadripolar spindle such as was described by FARMER (**28**, **29**, **30**, **31**) for Pallavicinia and some other forms of Hepaticae, and has been called in question by DAVIS (**19**) and MOORE (**50**, **51**).

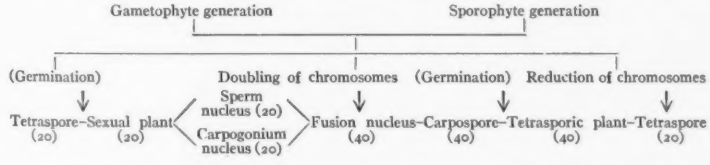
ALTERNATION OF GENERATIONS.

Alternation of generations.—Judging from the studies of Polysiphonia presented above, the male and female plants with their 20 chromosomes are gametophytes. The union of the male and female nuclei results in the fertilized carpogonium with the double number of chromosomes (40), marking the beginning of a new phase, the sporophyte generation. This fusion nucleus gives rise to a series of mitoses in the central cell of the cystocarp, all characterized by the double number of chromosomes, and consequently sporophytic in character, and carpospores are finally formed. The carpospore on germination presents the same number of chromosomes (40), and the successive mitoses following contain this number, so that the sporeling developed from the carpospore is still a part of the sporophytic phase. It may never be possible to grow such sporelings to maturity under experimental conditions, but it is evident that the plant developed from the carpospore must have nuclei with 40 chromosomes, until there is some marked change in the life history. The only vegetative form of Polysiphonia with 40 chromosomes is the tetrasporic plant, from which it must be inferred that the tetrasporic plant arises from

the carpospore and constitutes a part of the sporophyte generation that begins with the fertilized carpogonium .

This long sporophytic phase terminates with the formation of tetraspores, when a reduction of chromosomes takes place, 20 chromosomes entering each tetraspore. These tetraspores with the reduced number of chromosomes evidently have returned, with respect to nuclear conditions, to the potentialities of the original gametophyte or sexual generation. Again, it may never be possible to grow sporelings from the tetraspore to maturity under experimental conditions, but it is evident that plants derived from the tetraspores must have nuclei with 20 chromosomes. The sexual plants of Polysiphonia are the only forms in which 20 chromosomes are found, therefore it may safely be concluded that the sexual plants arise from tetraspores. The tetraspore then constitutes an indispensable part of the life history of Polysiphonia, and cannot be regarded simply as an accessory type of reproductive structure, such as is illustrated by many forms of asexual spores in the thallophytes or by the gemmae of bryophytes.

To summarize the life history of Polysiphonia, the gametophyte generation begins with the tetraspores and ends with the sexual cells or gametes, whose fusion initiates the sporophyte generation; this covers a long period, including the formation of carpospores, germination of carpospores, development of the tetrasporic plants, and at last ends with the formation of tetraspores. In other words, the sexual plants and the tetrasporic plants present the two distinct phases of an antithetic alternation of generations, with the cystocarp a part of the sporophytic phase, The life history of Polysiphonia may be tabulated as follows:



Taking up the theories concerning the life history of the red algae, OLTMANNS (**55**) concluded eight years ago, from an investigation of four genera (Dudresnaya, Gloeosiphonia, Callithamnion, and Dasya), that the structure derived from the fertilized carpogonium

is comparable to the sporophyte generation of the higher plants. At that time he expressed his opinion definitely that the tetraspore is a special form of reproductive cell, comparable to brood cells or gemmae, and with no fixed place in the life history. However, during the last year (**56**, p. 273) he has admitted the possibilities of reduction phenomena during tetraspore formation.

DAVIS (**24**, pp. 467, 471) in the same year definitely suggested the probability that reduction phenomena would be found in the tetraspore mother cell.

WILLIAMS (**81**) discovered chromosome reduction during tetraspore formation in Dictyota, which led him to conclude that the tetrasporic plant in Dictyotaceae is a sporophyte generation derived from the fertilized egg.

WOLFE (**86**) showed for Nemalion that the cells of the cystocarp have double the number of chromosomes found in the sexual plant, thus presenting the first cytological evidence that the cystocarp of the red algae is sporophytic in character. He places the period of chromosome reduction at the time of carpospore formation, basing his conclusion on a count of chromosomes in the mitosis just previous to the formation of the carpospores. However, he did not report the phenomena characteristic of chromosome reduction, namely the period of synapsis followed by the two mitoses which distribute the chromosomes so as to give a numerical reduction.

Recently STRASBURGER (**75**) has published his views concerning the alternation of generations in the brown algae, remarking that the tetraspores of the red algae seem to be different from those of the Dictyotaceae, and that the place of the chromosome reduction in the red algae should be sought elsewhere than at tetraspore formation, because some of the red algae develop no tetraspores, but instead form monospores. It is true that in some groups of red algae tetraspores are never formed, and in certain of these monospores are present. In these cases chromosome reduction may take place with the formation of the carpospores, or perhaps with their germination, and the monospore when present may have no vital relation to the main cycle of the life history. The group of the red algae is very large and contains a great variety of forms, with a wide range in the complexity of the cystocarp and the vegetative forms, so that it is

reasonable to expect important differences in the position of the period of chromosome reduction.

Origin of the tetraspore.—The simplest genera of the red algae, such as Lemanea, Batrachospermum, Chantransia, and Nemalion, have no tetraspores, but some of them have monospores, as in Chantransia and Batrachospermum (including the Chantransia form). In these types the period of chromosome reduction may be associated with the carpospore, either just before its development or at the time of its germination. The monospores, then, in such genera are not vitally concerned with the life history, and indeed are present upon the gametophyte. The tetrasporic plant may have arisen by a suppression of the reduction phenomena in connection with the carpospore, so that it germinates with the sporophytic number of chromosomes, producing a plant with this number, which consequently becomes at once a part of the sporophytic phase. The period of chromosome reduction would be thus postponed from the carpospore to a later period in connection with the newly formed plant. Such plants by developing tetraspores would end the sporophyte generation. It is quite possible that the first tetraspore mother cells corresponded to monospores on the sexual plants except that they had the double number of chromosomes, since such reproductive cells would very naturally become the seat of the delayed reduction phenomena. The resemblance in general morphology of the tetrasporic plants in the red algae to the sexual plants would be expected, because they live under similar environmental conditions, and we have another illustration of such similarity of gametophytes and sporophytes in the Dictyotaceae.

Abnormalities of the nature of monospores.—It should be remembered that sexual plants (cystocarpic) of Polysiphonia occasionally develop an abnormality in the form of a cell resembling a monospore but having the same cell lineage as the tetraspore mother cell. This abnormality may indeed be a reversion to an ancestral type of monospore, that in the process of evolution has given place to the tetraspore mother cell, which is only found in the sporophytic generation. It may be, however, simply an exceptional condition without any phylogenetic significance.

SUMMARY.

The nuclear conditions in the life history of *Polysiphonia violacea* may be summarized as follows:

1. The carpospore on germination shows 40 chromosomes, and 40 chromosomes appear in the vegetative mitoses of the tetrasporic plant; so it may be inferred that the tetrasporic plants come from carpospores.

2. The tetraspore on germination shows 20 chromosomes, and 20 chromosomes appear in the vegetative mitoses of the sexual plant; so it may be inferred that the sexual plants come from tetraspores.

3. The nuclei of the gametes (sperm and carpogonium) contain each 20 chromosomes. The fusion nucleus (sporophytic) in the fertilized carpogonium as a result has 40 chromosomes and gives rise to a series of nuclei in the central cell. Some of these enter the carpospores, which are consequently a part of the sporophytic phase to be continued in the tetrasporic plant. The gametophyte nuclei in the central cell of the cystocarp with 20 chromosomes break down.

4. Tetraspore formation terminates the sporophytic phase with typical reduction phenomena, so that the tetraspores are prepared to develop the gametophyte generation.

5. There is thus an alternation of a sexual plant (gametophyte) with a tetrasporic plant (sporophyte) in the life history of Polysiphonia, the cystocarp being included as an early part of the sporophytic phase.

THE UNIVERSITY OF CHICAGO.

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EXPLANATION OF PLATES XIX–XXVIII.

The figures were drawn with the aid of an Abbé camera lucida, under Zeiss apochromatic obj. 1.5^{mm} N. A. 1.30, combined with compensating ocular 18; except *figs. 13, 14, 133, 134* drawn with compensating ocular 12; *figs. 103, 109, 114–118, 124, 126, 132, 135, 163–171* drawn with ocular 4; and *figs. 65a, 74a, 147a,–153a, 171a'* drawn with compensating ocular 18 under higher magnification obtained when the tube was extended to the furthest point. The plates are reduced one-half the original size, except *plates XXI, XXII* and *XXVIII*, which are reduced two-fifths.

PLATE XIX.

The first mitosis in the germinating tetraspore.

FIG. 1. Nucleus in resting stage, showing delicate linin network and nucleolus.

FIGS. 2a–2c. Three sections of the same nucleus, showing segregation of chromatin material into about 20 groups, probably prochromosomes, before the formation of chromosomes.

FIGS. 3a, 3b. Two sections of the same nucleus, early prophase; 20 chromosomes may be counted.

FIG. 4. The late prophase; centrosome-like bodies lying at each pole.

FIG. 5. Metaphase showing equatorial plate; nuclear membrane still present; neuclear cavity considerably smaller than in the preceding stage.

FIG. 6. Membrane dissolving; centrosphere-like structures present at the poles of the spindle.

FIG. 7. The polar view of an equatorial plate showing 20 chromosomes and the remains of nucleolar material.

FIG. 8. Anaphase, showing groups of daughter chromosomes assembled at the poles of the spindle.

FIG. 9. Late anaphase, the original nuclear membrane entirely dissolved; centrosphere-like structures passing into vaguely outlined kinoplasmic masses.

FIG. 10. Polar view of late anaphase; space within the group of chromosomes probably indicates the first appearance of nuclear sap within a vacuole.

FIG. 11. Telophase; the membrane of the daughter nucleus is clearly formed.

FIG. 12. Resting condition of daughter nucleus, showing linin network and two nucleoli.

FIG. 13. Cleavage furrow appearing at the periphery of the cell in the middle region.

FIG. 14. The cleavage furrow has penetrated almost to the center of the cell, leaving only a narrow passage admitting of protoplasmic continuity between the daughter cells.

PLATE XX.

The first mitosis in the germinating carpospore.

FIG. 15. Nucleus in the resting condition, showing linin network.

FIGS. 16a–16c. Three sections of the same nucleus, showing 40 prochromosomes.

FIGS. 17a, 17b. Two sections of the same nucleus, early prophase; 40 chromosomes are formed.

FIGS. 18a, 18b. Two sections of the same nucleus; centrosome-like bodies occupying pole.

FIG. 19. Metaphase showing equatorial plate; centrosphere-like structures at the poles of spindle.

FIG. 20. Polar view of an equatorial plate showing group of 40 chromosomes and the remains of nucleolar material.

FIG. 21. Anaphase; groups of daughter chromosomes become assembled at the poles of the spindle.

FIG. 22. Later anaphase; original nuclear membrane entirely dissolved; centrosphere-like structures passing into vaguely outlined protoplasmic masses.

FIGS. 23a, 23b. Two sections of the same daughter nucleus in late anaphase viewed from the pole, showing early stage in development of the vacuoles containing nuclear sap.

FIGS. 24–24c. Three sections of the same daughter nucleus shortly after telophase; nuclear membrane clearly formed and two nucleoli present.

FIG. 25. Resting condition of daughter nucleus, showing linin network and nucleolus.

PLATE XXI.

Mitosis in the vegetative cells of the male plant.

FIG. 26. Apical cell of main filament; resting nucleus of an apical cell, showing linin network.

FIG. 27. The same; network becoming coarser.

Figs. 28–35. Apical cells of developing hairs.

FIG. 28. Chromatin granules aggregated into 20 prochromosomes.

FIG. 29. Prophase; 20 chromosomes clearly present; a centrosome-like body at each pole.

FIG. 30. Metaphase showing equatorial plate; centrosphere-like structures at the poles of spindle.

FIG. 31. The polar view of equatorial plate showing 20 chromosomes.

FIG. 32. Late metaphase; two groups of daughter chromosomes just separating.

FIG. 33. Anaphase; two groups of daughter chromosomes separated by a large vacuole which enters between them.

FIG. 34. Telophase; nuclear membrane around the daughter nuclei.

FIG. 35. Later stage than the previous figure; cleavage furrow proceeding inward so as to divide the apical cell.

Mitosis in the vegetative cells of female plants.

Figs. 36–42. Apical cells of developing hairs.

FIG. 36. Prophase of nucleus; centrosome-like body present at the pole.

FIG. 37. Metaphase, showing equatorial plate; centrosphere-like structure conspicuous.

FIG. 38. The polar view of metaphase.

FIG. 39. Late metaphase.

FIG. 40. Anaphase.

FIG. 41. Anaphase; the vacuole beginning to intrude between the groups of daughter chromosomes.

FIG. 42. Telophase; cleavage furrow appearing between the two daughter nuclei.

FIG. 43. Mitotic figure in the old region of thallus, showing large centrosphere-like structures.

FIG. 44. Polar view of the same stage as the above, showing 20 chromosomes.

Mitosis in the vegetative cells of the tetrasporic plant.

Figs. 45–51. All apical cells of main filament.

FIG. 45. Resting nucleus, showing linin network.

FIG. 46. Chromatin granules commence to aggregate to form prochromosomes.

FIG. 47. Early prophase showing 40 chromosomes.

FIG. 48. Metaphase showing equatorial plate; centrosphere-like structures present.

FIG. 49. Late metaphase; groups of daughter chromosomes separated.

FIG. 50. Polar view of metaphase showing 40 chromosomes.

FIG. 51. Anaphase; vacuole intruding between two groups of daughter chromosomes.

PLATE XXII.

Spermatogenesis.

Figs. 52–61. Formation of the sperm mother cell.

FIG 52. Terminal portion of a very young antheridium, consisting of an axial siphon of three cells; the nucleus of the lower cell is in a resting condition; the middle one in early prophase; and the upper one in anaphase.

FIG. 53. Mitotic figure in a cell of the axial siphon to form a stalk cell laterally.

FIG. 54. A cell of the axial siphon with the stalk cell formed laterally.

FIG. 55. Prophase in the stalk cell showing 20 chromosomes.

FIG. 56. Metaphase showing equatorial plate; centrosphere-like structures present.

FIG. 57. Polar view of the same stage as in the preceding figure, showing 20 chromosomes.

FIG. 58. Late metaphase stage; nuclear membrane still present.

FIG. 59. Anaphase; vacuole intruding between two groups of daughter chromosomes.

Fig. 60. Still later stage of anaphase.

FIG. 61. Telophase; cleavage furrow separating the sperm mother cell from the stalk cell.

Figs. 62–74. Formation of the first sperm.

FIG. 62. Resting nucleus of sperm mother cell, showing linin network.

FIG. 63. Fine reticulum transformed into 20 prochromosomes.

FIG. 63a. Portion of *fig. 63* under higher magnification.

FIG. 64. Prophase; a few spindle fibers attached to the chromosomes; centrosome-like bodies at the poles.

FIG. 64a. Portion of *fig. 64* under higher magnification.

FIG. 65. Metaphase; the centrosphere-like structures evident.

FIG. 65a. The nucleus of *fig. 65* under higher magnification.

FIG. 66. The polar view of the stage shown in the previous figure; 20 chromosomes clearly present.

FIG. 67. Late metaphase.

FIG. 68. Anaphase; vacuole intruding between the two groups of daughter chromosomes.

FIG. 69. Later stage of anaphase.

FIG. 70. Lower nucleus passing into resting condition.

FIG. 71. Cleavage furrow separates the sperm above from the sperm mother cell which is destined to produce later a second sperm.

FIG. 72. Sperm almost formed; the sperm mother cell beginning to elongate, preliminary to the development of a second sperm

FIG. 73. Side view of mature sperm

FIG. 74. Sperm viewed from above; chromosomes maintaining their individual forms.

FIG. 74a. Portion of *fig. 74* under higher magnification.

Figs. 75–81. Formation of the second sperm.

FIG. 75. Prophase of mitosis to form second sperm; the first sperm still present at the side, so that the sperm mother cell assumes an asymmetrical outline.

FIG. 76. Metaphase showing equatorial plate; centrosphere-like structures present.

FIG 77. Polar view of same stage as in previous figure.

FIG. 78. Late metaphase.

FIG. 79. Anaphase.

FIG. 80. Later anaphase; vacuole between the two groups of daughter chromosomes.

FIG. 81. Cleavage furrow separating the second sperm from the sperm mother-cell.

PLATE XXIII.

The formation of the procarp.

FIG. 82. Mitotic figure in the cell of the central siphon of a procarp, to form the first peripheral cell; centrosphere-like structures present.

FIG. 83. Polar view of the same mitosis, showing 20 chromosomes.

FIG. 84. First peripheral cell is formed.

FIG. 85. Mitosis to form second peripheral cell.

FIG. 86. Polar view of the same mitosis; 20 chromosomes present.

FIG. 87. Anaphase of the same mitosis.

FIG. 88. The fifth peripheral cell, called the pericentral cell, formed on the left of the central siphon; this cell is destined to develop the carpogonial branch.

FIG. 89. Mitosis to form first cell of the carpogonial branch from the pericentral cell.

FIG. 90. Polar view of the same stage as the previous figures, showing 20 chromosomes.

FIG. 91. Anaphase.

FIG. 92. Late anaphase.

FIG. 93. Telophase; vacuole intruding between the daughter nuclei.

FIG. 94. Mitotic figure to form second cell of the carpogonial branch; *pc*, pericentral cell.

FIG. 95. Polar view of the same stage as shown in the previous figure; 20 chromosomes readily seen.

FIG. 96. Mitotic figure forming the third cell of the carpogonial branch.

FIG. 97. Polar view of the same stage.

FIG. 98. Mitotic figure to form the fourth cell of the carpogonial branch.

FIG. 99. Polar view of the previous figure.

FIG. 100. Mitosis of the nucleus within the fourth cell of carpogonial branch, which develop the trichogyne and carpogonium; this mitosis gives two daughter nuclei as shown in *fig. 101*; being cut obliquely, the chromosomes, 20 in number, may be counted.

FIG. 101. The two nuclei within the carpogonium or the fourth cell of the carpogonial branch: *pc*, pericentral cell.

PLATE XXIV.

Development of the trichogyne.

FIG. 102. Development of the trichogyne from the carpogonium.

FIG. 103. A mature procarp in section, showing the situation of the carpogonial branch: *pc*, pericentral cell; *as*, axial siphon.

FIG. 104. Carpogonium with trichogyne at maturity; note the difference in size between the sister nuclei, for the carpogonium with its nucleus has enlarged greatly.

Fertilization.

FIG. 105. Sperm attached at the tip of the trichogyne.

FIG. 106. Contacts of sperm, its nucleus passing into trichogyne; note the individual chromosomes in the sperm nucleus.

FIG. 107. Sperm cell emptied of contents; sperm nucleus about to pass the trichogyne nucleus.

FIG. 108. Sperm nucleus having passed the trichogyne nucleus is about to enter the carpogonium.

FIG. 109. Section of procarp showing the situation of the carpogonium at the time of fertilization.

FIG. 109a. The carpogonium of *fig. 109* under higher magnification; sperm nucleus about to fuse with the female nucleus, which has moved upwards in the carpogonium.

FIG. 110. Mitotic figure in the formation of an auxiliary cell from the pericentral cell, which takes place parallel with the nuclear fusion in the carpogonium.

FIG. 111. Prophase of the above mitosis showing 20 chromosomes.

FIG. 112. Mitosis in a cortical cell of the procarp.

FIG. 113. Polar view of the above mitosis, showing 20 chromosomes.

FIG. 114. Section of procarp showing situation of the carpogonium at the time of contact between the sperm and carpogonium nuclei.

FIG. 114a. The carpogonium of *fig. 114* under higher magnification; the sperm nucleus beginning to fuse with the female; no membrane observable around the sperm nucleus since the beginning of entry of it into the trichogyne; the female nucleus in resting condition.

FIG. 115. Section of procarp showing carpogonium at a late stage in the fusion of the sexual nuclei.

FIG. 115a. The carpogonium of *fig. 115* under higher magnification; the chromosomes of the sperm nucleus beginning to separate in the female nucleus; the network in female nucleus preparing to form chromosomes.

FIG. 116. The fusion nucleus in the carpogonium after the female chromosomes have been formed, showing a mingling of male and female; the total number of chromosomes is 40.

Development of the cystocarp.

FIG. 117. Section of procarp at the time of the first mitosis of the fusion nucleus within the carpogonium.

FIG. 117a. The carpogonium of *fig. 117* under higher magnification, showing the first mitosis of the fusion nucleus.

FIG. 118. Procarp showing the first mitosis of the fusion nucleus in the carpogonium; cut obliquely.

FIG. 118a. The carpogonium of *fig. 118* under higher magnification, showing a polar view of first mitosis of the fusion nucleus; 40 chromosomes present.

FIG. 119. Prophase of a nucleus within the first cell of the carpogonial branch.

FIG. 120. Metaphase of the above mitosis.

FIG. 121. Polar view of the same mitosis showing 20 chromosomes.

FIG. 122. Anaphase of the same mitosis.

PLATE XXV.

FIGS. 123a, 123b. Two sections of the fusion nucleus at metaphase of the first mitosis.

FIG. 124. Section of the procarp at anaphase of the first mitosis of the fusion nucleus within the carpogonium.

FIG. 124a. The carpogonium of *fig. 124* under higher magnification.

FIG. 125. Migration of one of two daughter nuclei (sporophytic), resulting from the first mitosis of the fusion nucleus, into the third auxiliary cell (compare with *a3* in *diagram 3*).

FIG. 126. Migration of two daughter nuclei (sporophytic) into the pericentral cell, the third auxiliary cell having fused with it; a nucleus from one of the auxiliary cells below also entering the pericentral cell; the first, second, and third cells of the carpogonial branch, together with the carpogonium, about to collapse.

FIG. 127. Mitoses of two sporophytic nuclei derived from the fusion nucleus and of a gametophytic nucleus also within the central cell; the distinction between

the mitotic figures is readily seen by estimating the number of chromosomes arranged in the equatorial plate.

FIG. 128. Sporophytic nucleus in a process from the central cell, from which after a mitosis a carpospore will be formed; the nucleus in prophase; 40 chromosomes may be counted.

FIG. 129. Metaphase of the mitosis which separates the carpospore from the stalk cell.

FIG. 130. Polar view of the same mitosis cut obliquely, showing 40 chromosomes.

FIG. 131. Telophase of the same mitosis; the upper nucleus will lie in the carpospore.

FIG. 132. Section of a cystocarp, showing central cell (*cc*), stalk cell (*sc*), carpospore (*sp*), and paranematal filaments (*pf*).

FIG. 133. Stalk cells beginning to fuse together side by side, and their nuclei, with other nuclei remaining in the central cell, beginning to disorganize.

FIG. 134. Disorganizing nuclei in the central cell.

FIGS. 135a–135d. Four sections of a procarp, showing the arrangement of the auxiliary cells (compare with *diagram 3*); the fusion nucleus in the carpogonium (*carp*) shows the mingling of male and female chromosomes.

PLATE XXVI.

The tetraspore formation.

FIG. 136. Prophase in a cell of the central siphon previous to the formation of pericentral cell, showing 40 chromosomes.

FIG. 137. Metaphase of this mitosis.

FIG. 138. Anaphase.

FIG. 139. Polar view of anaphase; 40 chromosomes present.

FIG. 140. Tip of a filament, showing stages in the formation of the tetraspore mother-cell; *pc*, pericentral cell; *sc*, stalk cell; *tmc*, tetraspore mother cell.

FIG. 141. Chromatin network in resting nucleus of pericentral cell.

FIG. 142. Metaphase of the mitosis in the pericentral cell; centrosphere-like structures present.

FIG. 143. Late metaphase of the same.

FIG. 144. Anaphase.

FIG. 145. Telophase; vacuole intruding between the daughter nuclei.

FIG. 146. Tetraspore mother cell becoming separated from the stalk cell by the cleavage furrow.

FIG. 147. Later stage of the above; tetraspore mother cell increased in size; the nucleus with delicate linin network.

FIG. 147a. Portion of linin reticulum in *fig. 147* under higher magnification.

FIG. 148. Reticulum becoming transformed into a coarser chromatin network with here and there large knots upon the threads.

FIG. 148a. Portion of network from *fig. 148* under higher magnification.

FIG. 149. Irregular network becoming transformed into more even threads.

FIG. 149a. Portion of threads from *fig. 149* under higher magnification.

FIG. 150. Threads becoming arranged parallel to one another.

FIG. 150a. Portion of threads from *fig. 150* under higher magnification.

FIG. 151. Synapsis.

FIG. 151a. Portion of the parallel threads from *fig. 151* fusing in parts, under higher magnification.

FIG. 152. Nucleus emerging from synapsis.

FIG. 152a. Portion of fused parallel threads or spirem from *fig. 152* under higher magnification; the spirem beginning to split longitudinally.

FIG. 153. Later stage than the above; spirem beginning to segment to form chromosomes; the split segments arranged side by side.

FIG. 153a. Segments of spirem from *fig. 153* under higher magnification, showing X and double L and V forms.

PLATE XXVII.

FIG. 154. Early prophase of mitosis in tetraspore mother cell; 20 bivalent chromosomes are present.

FIG. 154a. Chromosomes from *fig. 154* under higher magnification, showing bivalent character.

FIG. 155. Later prophase; bivalent chromosomes have been shortened.

FIG. 156. Metaphase; a great number of chromosomes (about 80) arranged in the equatorial plate; this large number results from the premature division of the halves of the bivalent chromosomes shown in *fig. 155;* the 80 chromosomes are therefore granddaughter chromosomes, which will be distributed to the four tetraspores; centrosphere-like structures poorly differentiated.

FIG. 157. Later metaphase of the first mitosis; two groups of daughter chromosomes, 40 in each, just separating and the four poles of second spindle already differentiated.

FIG. 158. Metaphase of second mitosis; four groups of granddaughter chromosomes (three seen) passing to the poles.

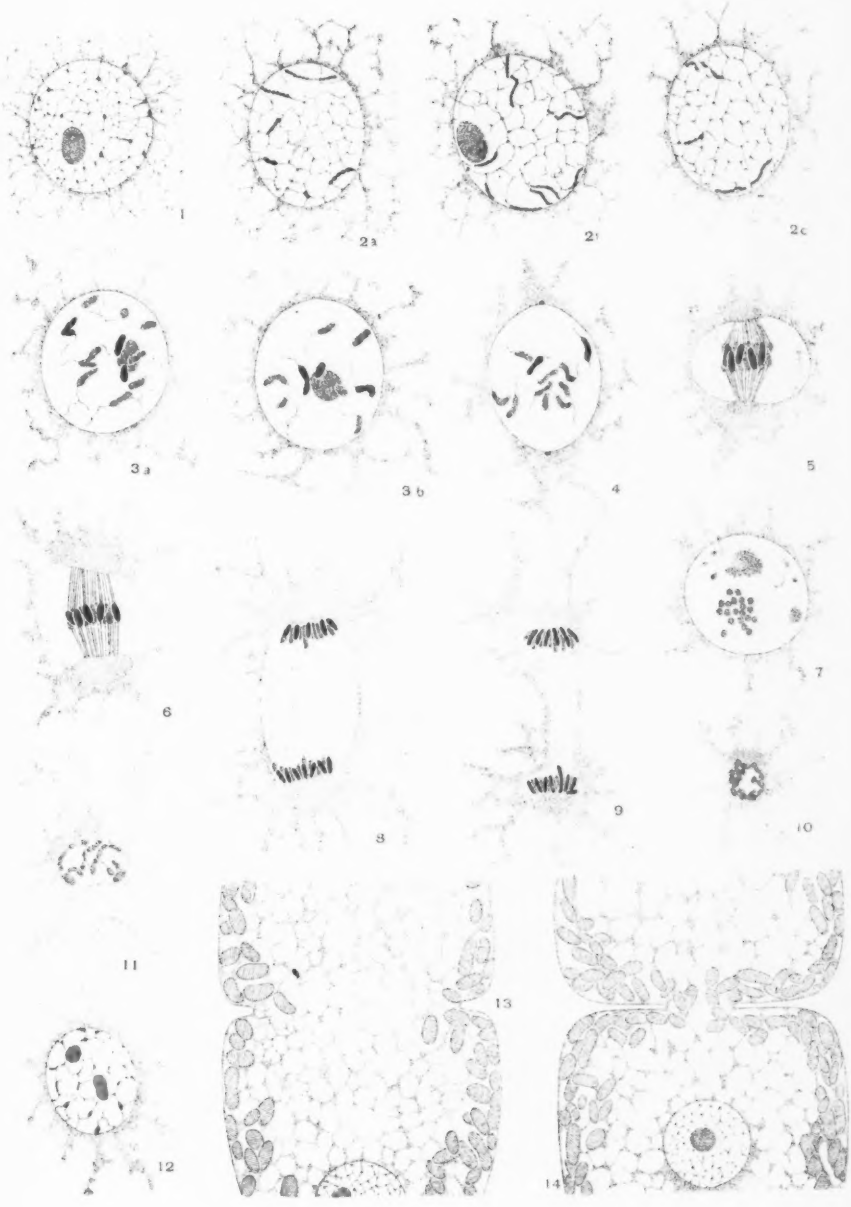
FIG. 159. Groups of granddaughter chromosomes at the poles; nucleolus has appeared in the center of the nuclear space.

FIG. 160. Groups of granddaughter chromosomes forming chromatin network; membrane surrounding the nuclear cavity assuming a tetrahedral shape with kinoplasm accumulating at the corners.

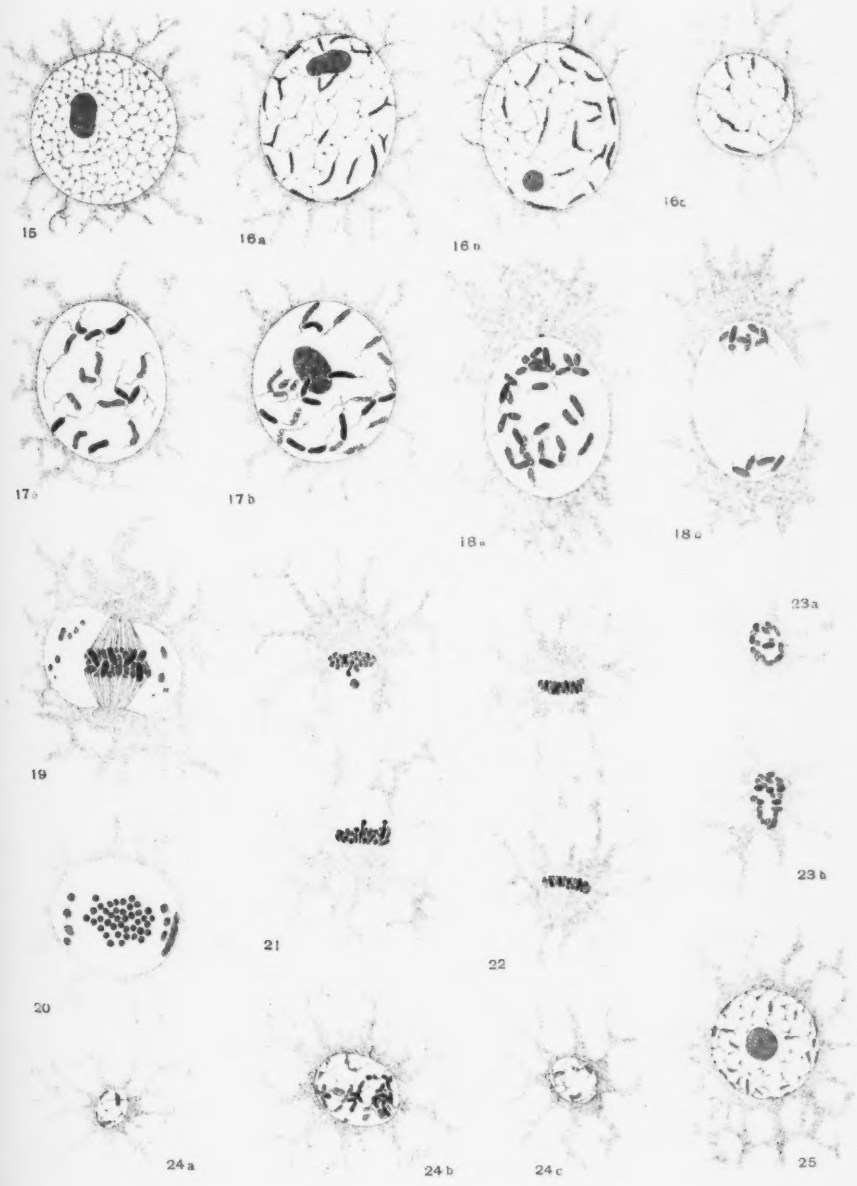
FIG. 161. Groups of granddaughter chromosomes have formed an anastomosing chromatin network; membrane surrounding nuclear cavity has broken in the region between the four poles so as to admit the entrance of kinoplasmic fibrils without the membrane; the fibrils grow toward the center of the nuclear cavity.

FIG. 162. Daughter nuclei becoming separated by the growth of kinoplasm which surrounds the chromatin network.

FIG. 163. Tetraspore mother cell at the time of separation of the daughter nuclei.



YAMANOUCHI on POLYSIPHONIA



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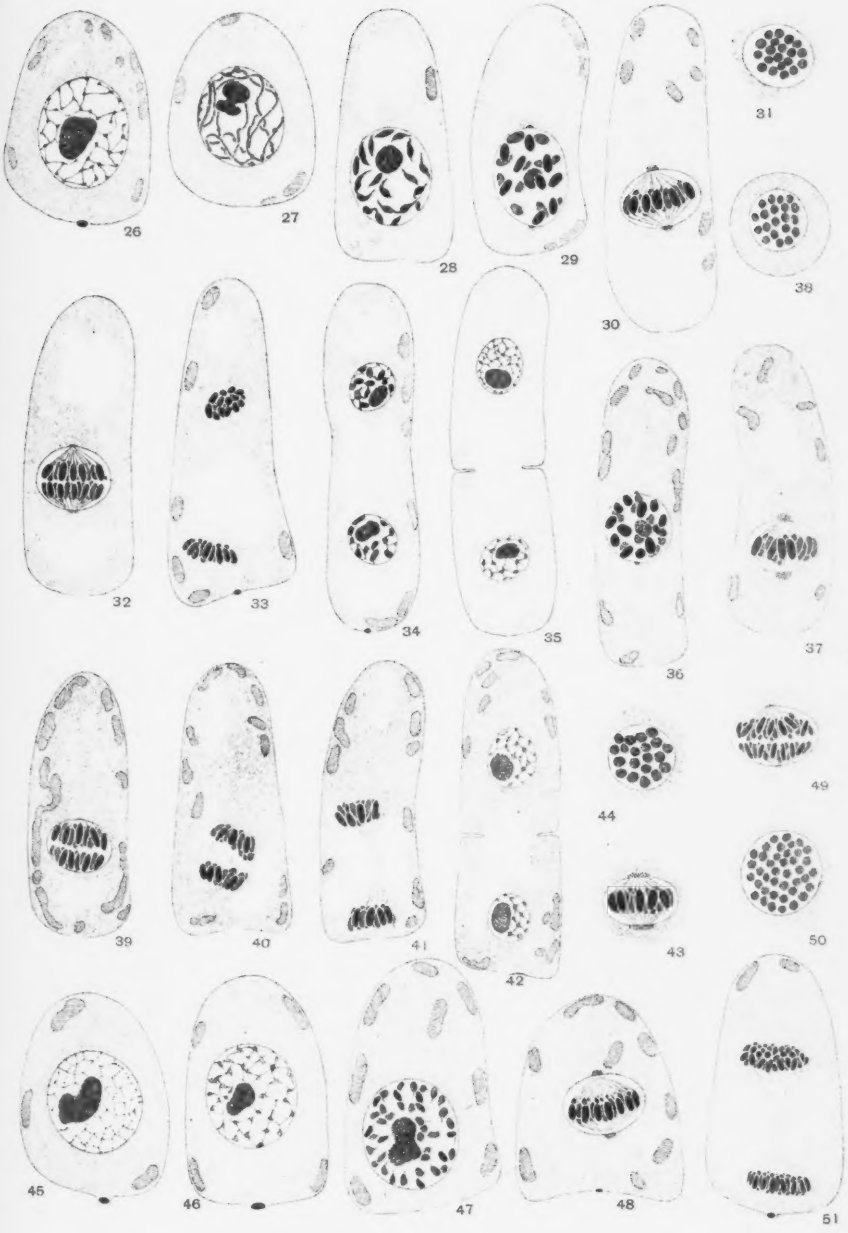

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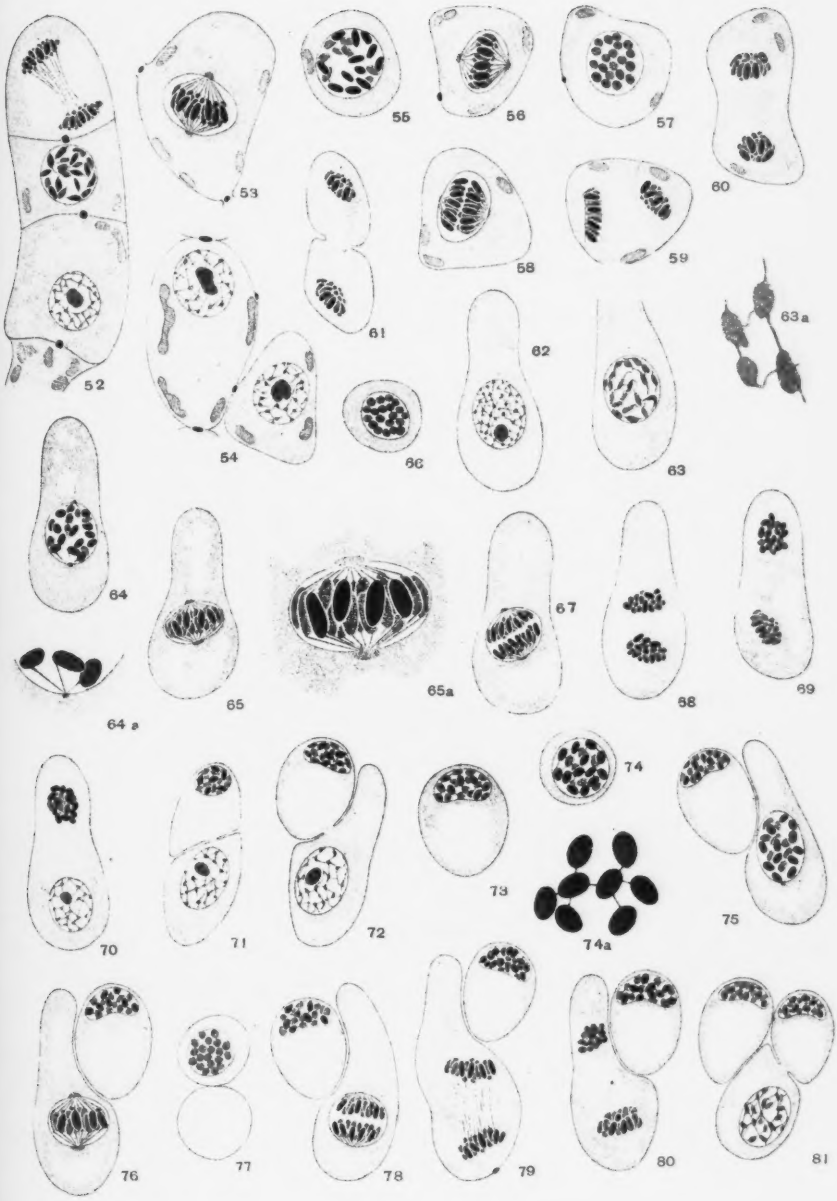
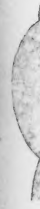
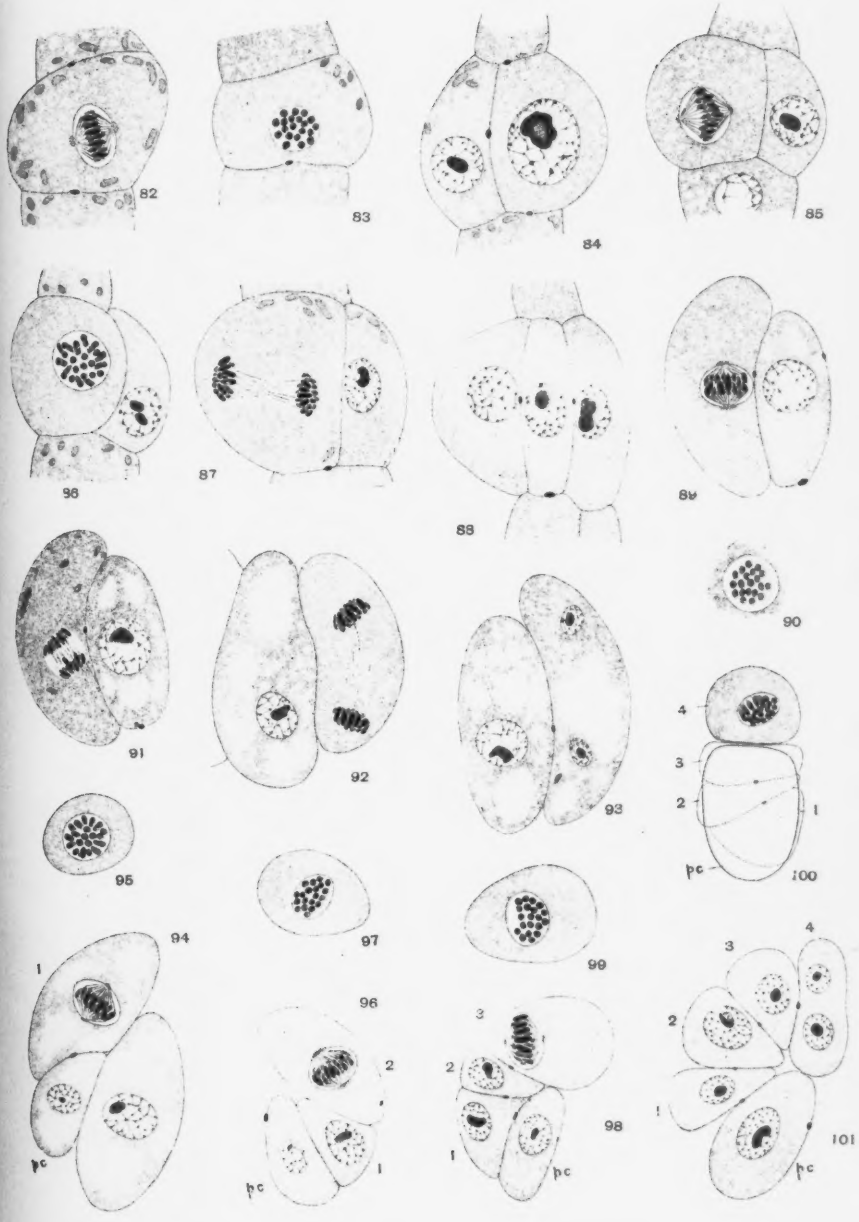


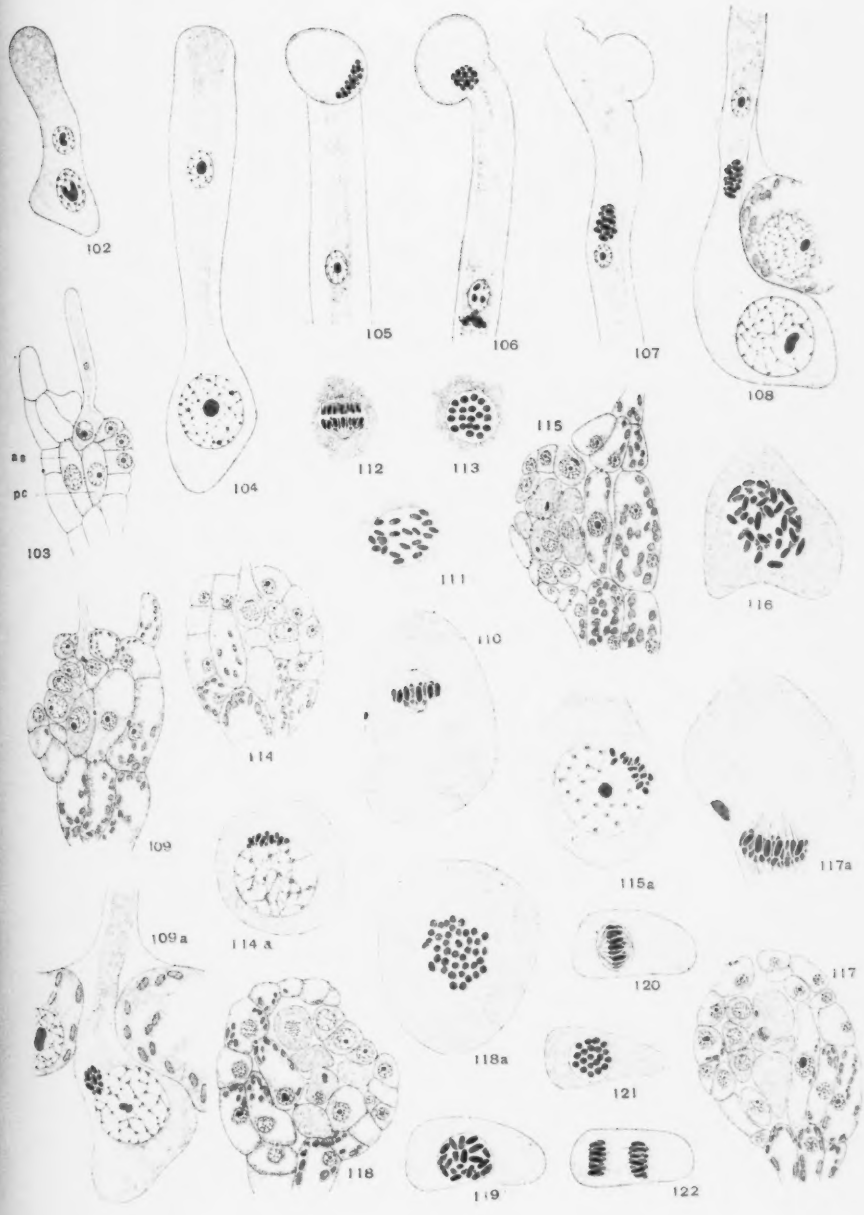
YAMANOUCHI on POLYSIPHONIA



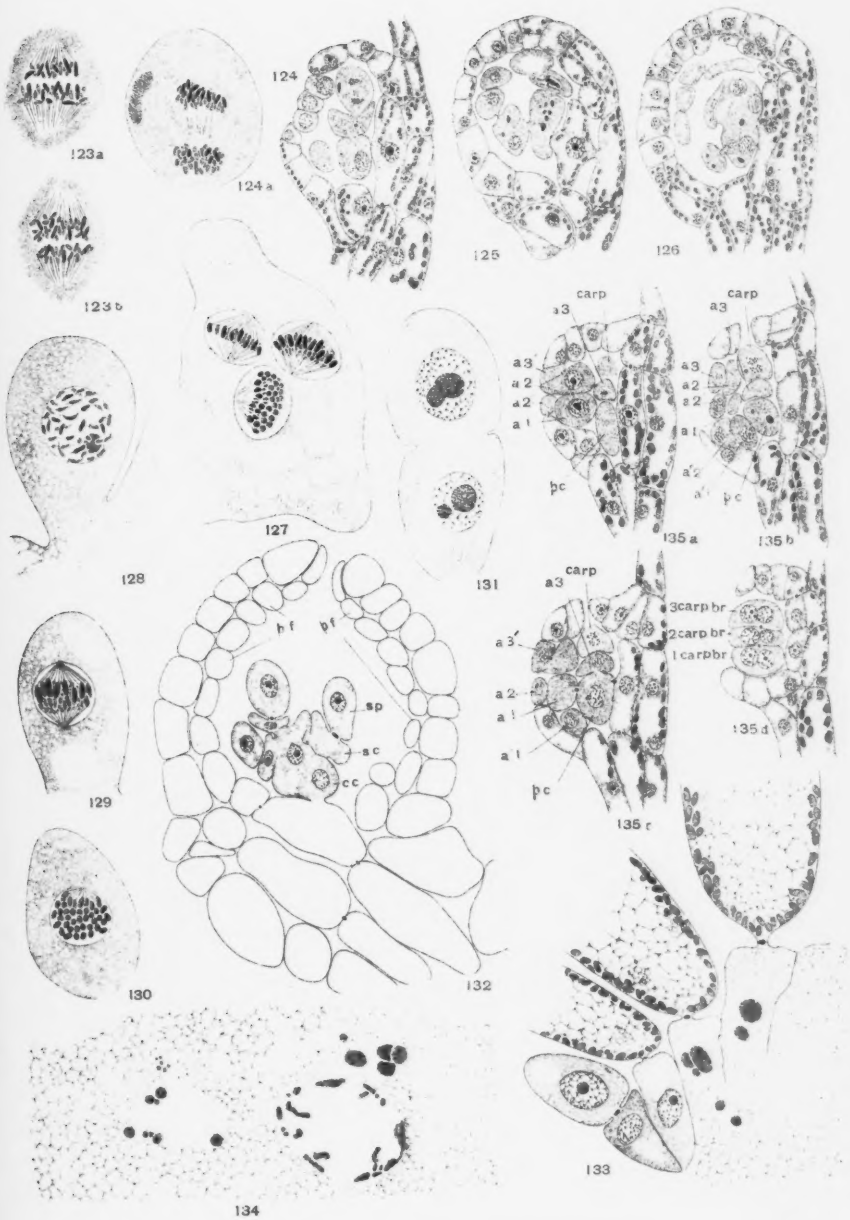


YAMANOUCHI on POLYSIPHONIA

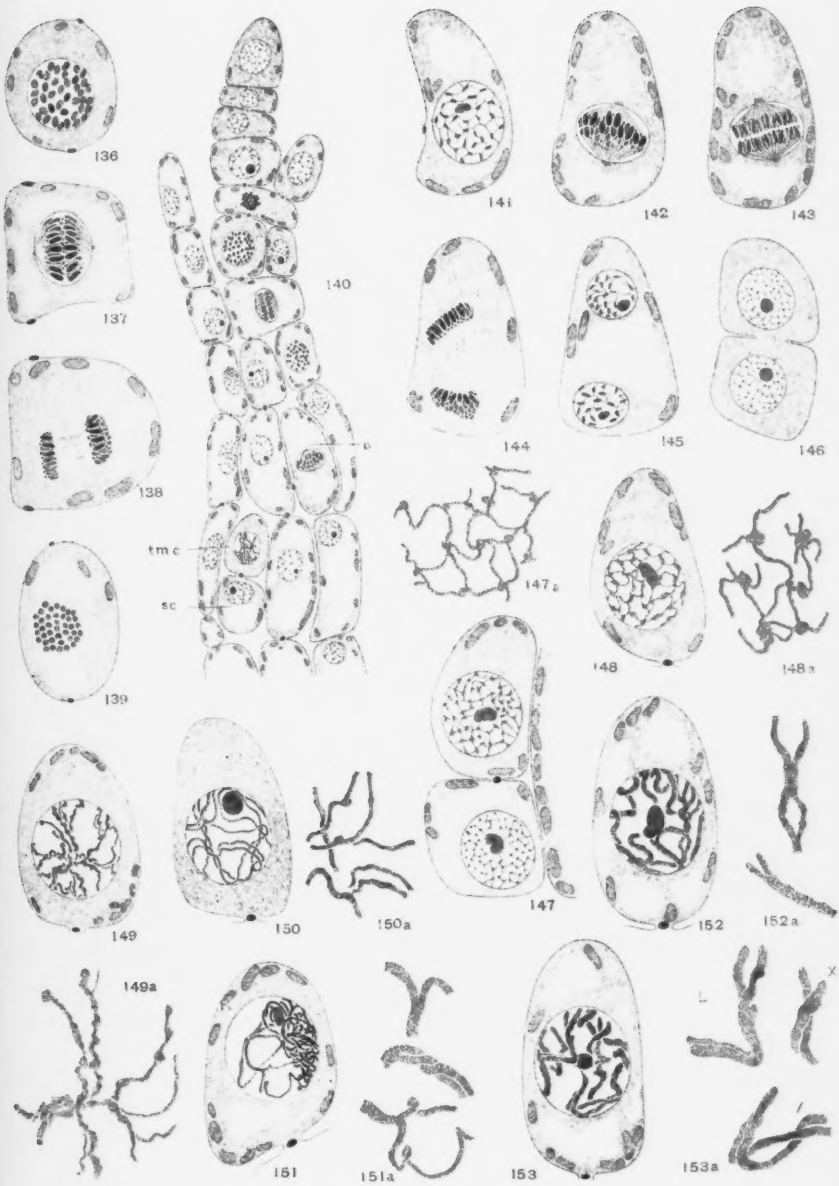
ag
pc



YAMANOUCHI on POLYSIPHONIA

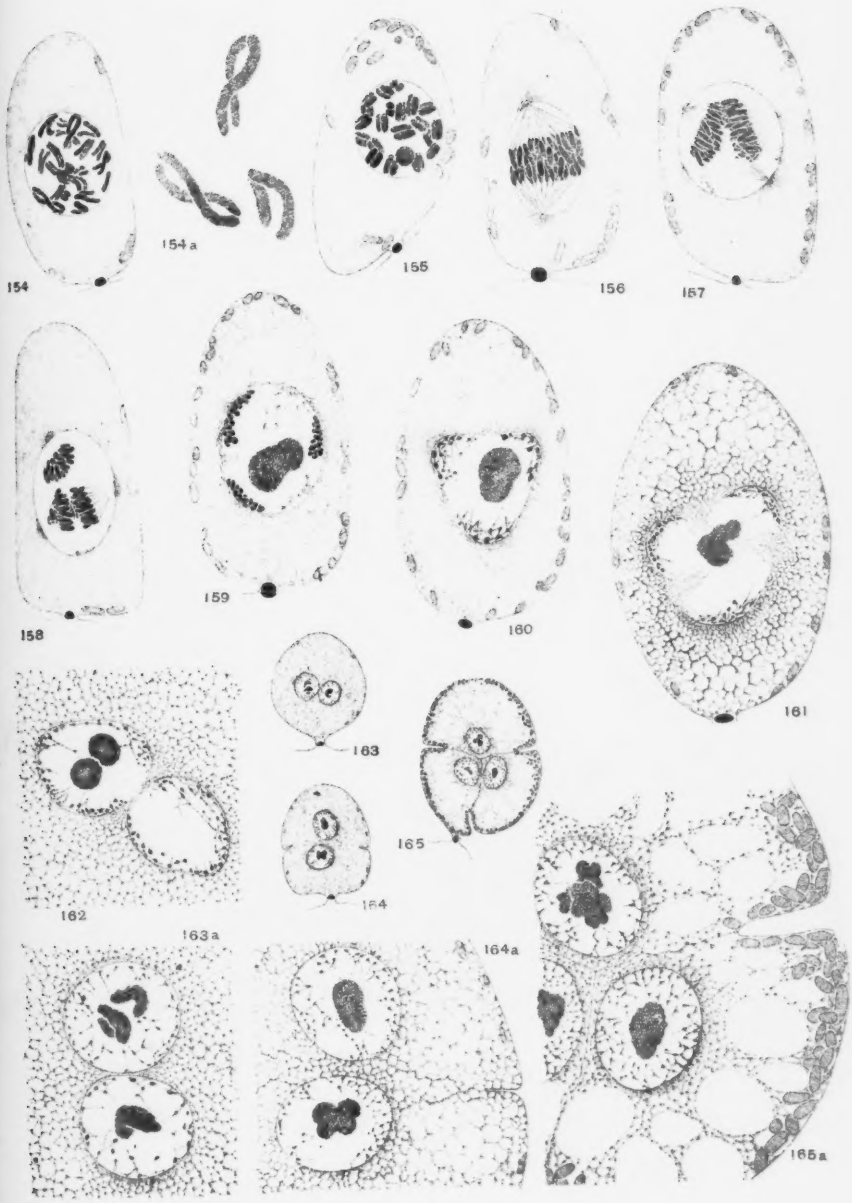


YAMANOUCHI on POLYSIPHONIA



YAMANOUCHII on POLYSIPHONIA

BOTA



YAMANOUCHI on POLYSIPHONIA

YAMANOUCHI on POLYSIPHONIA

FIG. 163a. The nuclei of *fig. 163* under higher magnification, showing their structure with linin network and nucleoli.

FIG. 164. The four daughter nuclei are completely formed (two visible); cleavage furrow appearing at the periphery.

FIG. 164a. Portion of *fig. 164* under higher magnification, showing details of cleavage furrows.

FIG. 165. Tetraspore mother cell with cleavage furrows growing towards the center.

FIG. 165a. Portion of *fig. 165* under higher magnification, showing the vacuolar structure and the progress of the cleavage furrows.

PLATE XXVIII.

Abnormalities.

FIG. 166. A young antheridium in which a stalk cell has increased in size and assumed the appearance of an auxiliary cell in the procarp.

FIG. 167. Showing the division of a stalk cell; the black spot within the cell indicates transverse section of protoplasmic strands connecting it with other stalk cells above or below.

FIG. 168. A cell formed on a sexual plant whose lineage is similar to that of the tetraspore mother cell.

FIG. 168a. This cell from *fig. 168* under higher magnification; the nucleus in a resting condition.

FIG. 169. Still later stage in the formation of this cell.

FIGS. 170a–170g. Seven sections of a similar cell; nucleus remains undivided, although the beginning of a cleavage furrow is present, which however never proceeds further.

FIG. 170d′. Nucleus of *fig. 170d* under higher magnification, in a resting condition.

FIG. 171. A rare case where the nucleus of this cell undergoes a typical mitosis.

FIG. 171a. The nucleus of *fig. 171* under higher magnification.

FIG. 171a′. The mitotic figure of *fig. 171a* under still higher magnification shows that this division is typical and that the daughter chromosomes are 20 in number in each group.

THE MORPHOLOGY OF THE ASCOCARP AND SPORE-FORMATION IN THE MANY-SPORED ASCI OF THECOTHEUS PELLETIER I.

JAMES BERTRAM OVERTON.

(WITH PLATES XXIX AND XXX)

ALTHOUGH free cell formation and spore formation have been thoroughly described by several authors, the process has not been followed in asci containing more than eight spores. In view of the old and widely held opinion that the ascus closes a sporophyte generation and is a spore mother cell, the study of the development of a many-spored ascus becomes especially important. The correlative phenomenon of the regular formation of eight nuclei in the ascus by a triple division, whether eight spores or less are to be formed, has been well established; but the variations from the typical method of spore formation and the necessary nuclear and cell divisions, by which more than eight spores are formed, are still in need of further study, and may prove valuable in aiding to solve the character of this peculiar organ. The presence of a true sexual process in the higher fungi, especially among the Ascomycetes, has been established beyond a doubt by the investigations of HARPER and others, but much still remains to be learned concerning the morphology of the sexual organs and ascogonia in the individual forms of this group.

The present investigation was undertaken during the past year, in order to determine the method of spore-formation in many-spored asci. *Thecotheus Pelletieri* presented itself as favorable material. Incidentally stages in the development of the ascocarp have been found which will also be described. The fungus agrees in general with the descriptions and figures of *Thecotheus Pelletieri* (Cr.) Boud., except that the asci are less conspicuously exserted than shown in the figures of CROUAN ('57), BOUDIER ('69), PATOUILLARD ('83), and REHM ('96), and the spores are also faintly colored. BOUDIER, to whom I have also sent material, has had the kindness to examine the fungus and has confirmed the determination, with the note, however, that he finds the spores somewhat larger than in the type.

As will be seen from the description below, the form differs from the species of Ryparobius described by BARKER (:03, :04) in having several ascogonia instead of a single one. As it may be found that this is a character of generic significance, I have thought best to follow BOUDIER in including this form under a separate generic name.

The investigation of the Ascomycetes has shown that there are great variations in the morphology and development of both fruit bodies and reproductive organs, and a sharp distinction may be made as to whether the sexual organs, associated with ascocarp formation, occur singly or in groups. Below I have brought together those forms whose fruit bodies develop from a single ascogonium, as contrasted with those whose ascocarps develop from several ascogonia. In strong contrast to these may also be added a third group of apparently apogamous forms, whose fruit bodies develop directly from a cell of the mycelium without the appearance of sexual organs.

I. In the following forms the ascocarps develop in connection with a single set of sexual organs: Monascus (BARKER :03, OLIVE :05), Dipodascus (JUEL :02), Gymnoascus (BARANETZKY '72, VAN TIEGHEM '76, '77, EIDAM '83, Miss DALE :03), *Erysiphe cichoraceaarum* (*Sphaerotheca castagnei*) (DEBARY '63, HARPER '95), *Erysiphe galeopsidis* (DEBARY '70), *Erysiphe communis* (DEBARY '70, HARPER '96), *Sphaerotheca humuli* (BLACKMAN & FRASER :05), *Phyllactinia corylea* (HARPER :05), perhaps *Eurotium repens*, *Aspergillus glaucus*, (DEBARY '70), *Penicillium glaucum* (BREFELD '74), *Aspergillus glaucus* (VAN TIEGHEM '77), Chaetomium (VAN TIEGHEM '75, '76, EIDAM '83, ZUKAL '86, OLTMANNS '87), *Stictosphaeria Hoffmanni*, with several species of Diatrype, Eutypa, Quaternaria, and Xylaria (FUISTING '67), *Sphaeria lemaneae*, *Sordaria fimiseda* (WORONIN '70, GILKENET '74), and *Ceratostoma brevirostre*, *Hypocopra* sp. (Miss NICHOLS '96). Among the Discomycetes the following investigated forms show a single ascogonium: *Ascobolus furfuraceus* (JANCZEWSKI '72, HARPER '96), *A. pulcherrimus* (WORONIN '66), *Ryparobius* sp. (BARKER :03, :04), *Peziza granulosa*, *Lachnea scutellata* (WORONIN '66), *Humaria granulata* (BLACKMAN & FRASER :06), *Ascodesmis nigricans* (VAN TIEGHEM '76), and *Thelebolus stercoreus* (RAMLOW :06).

II. *Pyronema confluens* (TULASNE '66, DEBARY '63, KIHLMAN '83, HARPER :00), several species of Collema (BAUR '98), *Parmelia*

acetabulum (BAUR :01, :04), *Anaptychia ciliaris*, *Lecanora subfusca*, *Endocarpon miniatum*, *Gyrophora cylindrica*, *Cladonia pyxidata* (BAUR :04), *Pertusaria communis*, *Pyrenula nitida* (BAUR :01), and *Boudiera Clausseni* (CLAUSSEN :05) represent the only forms thus far described in which the ascocarp is developed in connection with several ascogonia. As described below, Thecotheus also possesses a compound ascogonial apparatus from which the fructification originates.

III. In certain Pyrenomycetes ascocarp formation is apparently independent of sexual organs, being initiated by the formation of a parenchymatous mass of tissue, which is formed by the division of a single hyphal cell of the mycelium, as in Teichospora and Teichosporella (Miss NICHOLS '96) and also in Pleospora (BAUKE '77).

From the above list, selecting the best investigated forms which have a simple ascocarp, we find Dipodascus, Thelebolus, Gymnoascus, Sphaerotheca, Erysiphe, Phyllactinia, Ryparobius, Ascobolus, Humaria, and Monascus. Those having a compound apothecium are several species of lichens (in which, according to BAUR, several hundred carpogonia in some cases may be present in a single apothecium), Pyronema, Boudiera, and Thecotheus.

JUEL (:02) has studied the nuclear phenomena in Dipodascus. The sexual organs arise as short outgrowths of two neighboring cells, each gamete containing several nuclei. After the organs fuse, the walls between break down and the nuclei of the antheridium pass into the oogonium, which grows into a single ascus containing a large fusion nucleus and several smaller nuclei. Although JUEL was unable to make out the details of spore delimitation, he claims that the appearance of the cytoplasm indicates that the spores are formed by free cell formation about the descendants of the fusion nucleus, while the remaining nuclei, which did not fuse in the oogonium, lie scattered in the epiplasm. The actual process of nuclear fusion was not observed.

Miss DALE (:03) describes a sexual fusion of gamete cells in *Gymnoascus Reessii* and *G. candidus*. The oogonia and antheridia are of more or less separated origin. BARKER (:03), IKENO (:03), KUYPER (:04, :05), and OLIVE (:05) have investigated Monascus. BARKER'S and OLIVE'S accounts differ somewhat from that of IKENO. These two authors describe the ascogenous hyphae of Monascus

as arising from an oogonium which has been fertilized by an antheridium, thus establishing a sexual process for Monascus. They also hold that the asci arise from the cells of ascogenous hyphae; while IKENO asserts that there are no ascogenous hyphae, but that uninucleate spore mother cells arise by free cell formation, which in turn form spores also by free cell formation. KUYPER denies any fusion of sexual cells in Monascus, mainly confirms IKENO's observations, and regards the spore mother cells as true asci.

Two forms closely related to Thecotheus in that they belong among the Ascobolaceae have been investigated. BARKER (:**03**, :**04**) in two preliminary notes has described the presence of sexual organs in Ryparobius. The development of the ascocarps was observed step by step under the microscope in hanging drop cultures. The archicarp consists of a small coiled oogonium and a slender antheridium arising from the next cell of the mycelium, growing out over the tip of the oogonium, and fusing at the point of contact. Both antheridium and oogonium are uninucleate when first formed, but subsequently nuclear division occurs in each organ. Nuclear fusion probably occurs, constituting a regular fertilization, although this process was not actually observed. Walls are formed, so that the resulting cells are uninucleate with the exception of the penultimate cell of the ascogonium, which is sometimes found to contain two nuclei lying close together. It will be seen that there is great similarity between Ascobolus and Ryparobius as to the morphology of both the ascogonia and the ascocarps. The ascogenous hyphae, however, do not originate from any particular cell of the ascogonium, as has been described for Ascobolus.

CLAUSSEN (:**05**) has also worked out the morphology of the ascocarp of a form which he at first believed to be *Boudiera hyperborea*, but which HENNINGS (:**03**) described as a new species under the name of *B. Clausseni*. CAVARA (:**05**), basing his conclusions upon CLAUSSEN's figures, descriptions, and culture methods, believes that this fungus is not a new species of Boudiera, as HENNINGS has described, but that it corresponds perfectly to a species of Ascodesmis, which has been described by VAN TIEGHEM ('**76**) and later by ZUKAL ('**86**). VAN TIEGHEM described in detail two species, *A. nigricans* and *A. aurea*. CAVARA believes that the fungus is *A. nigricans*

Van Tiegh., and that it has been found by him ('89) in the neighborhood of Pavia. DANGEARD (:03) has also briefly described the development of *A. nigricans*, which CAVARA fails to note. So far as I am able to judge from the figures and descriptions of these authors, I see no reason for doubting that CLAUSSEN's fungus represents a new species of Boudiera, as described by HENNINGS. CLAUSSEN grew the fungus on cultures and was able to trace the life history from spore to spore. He found that the archicarps consisted of antheridia and oogonia spirally coiled together and borne in groups. As in Pyronema, the apothecium originates from several pairs of gametes. The ascogenous hyphae appear to originate from any or all of the cells of the ascogonium.

The latest work of HARPER (:05), already referred to, traces the formation of the sexual organs and nuclear fusion in *Phyllactinia corylea* in the minutest detail, showing that the ascocarps develop as the result of fertilization.

BLACKMAN and FRASER (:06) point out that the non-cytological investigation of several forms has shown that a normal sexual process is not to be expected in all, and they have therefore undertaken the cytological investigation of *Humaria granulata*, a form in which no antheridium is present. They find that the oogonium develops as a side branch from multinucleate cells of the mycelium, but that no antheridia are formed as described by WORONIN ('66). The archicarp consists of a varied number of cells, the apical cell of which is much swollen and vacuolate, becoming the ascogonium. Investing hyphae arise from the stalk cells but no antheridia are developed. The ascogonial cell contains a number of nuclei probably formed by division of its primary nuclei. These female nuclei fuse in pairs, thus constituting what they regard as a reduced sexual process, similar to what occurs in the development of the aecidium of *Phragmidium violaceum*. This vegetative fusion occurs in the ascogonia of various ages, and at no definite stage as in Pyronema. These fusion nuclei pass into the ascogenous hyphae, and on account of their size are easily distinguished from those of the vegetative hyphae.

RAMLOW (:06) has shown that the archicarp of *Thelebolus stercoreus* arises as a much twisted uninucleate organ from the uninucleate cells of the mycelium. No antheridium is developed, but the nucleus

of the oogonium divides by successive division until eight free nuclei are formed. Cross walls are then formed in such a manner that one cell contains two nuclei. This cell is larger and finally develops a single ascus, as in Sphaerotheca. No reduced sexual fusion, such as described by BLACKMAN and FRASER, was observed, and RAMLOW believes that Thelebolus is strictly apogamous. Although this form has been placed among the Hemiasci by several earlier authors, RAMLOW from his studies believes it to be a member of the Ascobolaceae, as suggested by SCHROETER and REHM.

That a sexual reproduction occurs in the lichens, comparable to that found in the red algae, as first described by STAHL ('77), and confirmed by BORZI ('78) for other species of Collemaceae, has been practically established by the investigations of several later authors. Although KRABBE'S work ('83, '91) on Cladonia, Baeomyces, and Sphyridium would indicate that sexual organs were absent in these forms, yet WAINIO ('90, '97, '98) claims to have found trichogynes in very young podetia of Cladonia, which would show that sexual organs are present. BAUR'S work ('98) on *C. crispum* confirms STAHL'S observations in every detail. He figures and describes carpogonia and trichogynes. His work also shows that fertilization is a necessity to the development of asci. If the carpogonia are not fertilized by a spermatium, they develop vegetative hyphae; while each cell of the carpogonium which has been fertilized develops ascogenous hyphae. The discovery by STAHL and LINDAU ('88) of trichogynes in *Physcia pulverulenta* has been confirmed by DARBISHIRE ('99), who finds a trichogyne and a carpogonium, each cell of which is uninucleate. The cells of this carpogonium become connected so as to form a more or less continuous structure. LINDAU ('88, '89) has also described the presence of trichogynes in several other species of lichens, but denies that they are sexual organs. In a more recent work BAUR (:01) finds that *Parmelia acetabulum*, *Anaptychia ciliaris*, *Pertusaria communis*, and *Pyrenula nidia* have carpogonia. Anaptychia possesses a single carpogonium, while the other forms have the carpogonia in groups, thus making the fruit body a compound apothecium. BAUR'S opinion is that fertilization occurs by means of spermatia combining with the trichogynes. In a still more recent work BAUR (:04) finds the ascogenous hyphae of Parmelia, Anapty-

chia, Endocarpon, Gyrophora, Lecanora, and Cladonia arising from carpogonia similar to those of Collema, so that these forms also probably possess sexual organs. Solorina is probably apogamous, behaving in this respect like *Peltigera peltidea* and Nephromium as described by FÜNFSTÜCK (:**02**), in which trichogynes have disappeared. SCHULTE (:**04**) has studied the structure of several species of Usnea. In *U. longissima* he claims that the asci do not arise from the ascogonia, although several are present. Trichogynes and spermatia could not be found in *U. microcarpa*.

The presence of trichogynes, spermatia, and carpogonia similar to those of the red algae, and also ascogenous hyphae which arise from carpogonia, all indicate the presence of an undoubted functional sexual apparatus in the lichens, although the important phenomena relating to nuclear behavior still remain unsolved.

GUILLIERMOND (:**05**) has discovered a nuclear fusion accompanying cell fusion in certain yeasts which he holds to be sexual. Conjugation of conidia and nuclear fusion take place in the Schizosaccharomycetes and Zygosaccharomyces just before spore formation, while in certain other forms (*S. Ludwigii*, etc.) the same phenomena occur at the time of spore germination. In the Schizosaccharomycetes and Zygosaccharomyces two cells become connected by a conjugation tube in which nuclear fusion occurs. The fusion nucleus divides immediately and the two daughter nuclei separate, one entering each original cell, in which a double division occurs to form the four nuclei of the four so-called ascospores. In certain other yeasts, such as *S. Ludwigii*, projections are put out from contiguous spores in the ascus, fusing to form a canal in which nuclear fusion occurs. A promycelium is developed from this conjugation tube, which buds off conidia. GUILLIERMOND considers the phenomena here presented as the conjugation of isogamous gametes, in the one case before and in the other case after the formation of the asci. In the one case, *S. Ludwigii*, yeast of Johannisberg, and *S. saturnus*, the sporophyte with the double nuclear characters is the ordinary vegetative budding stage of the yeast, while in the other case (Schizosaccharomycetes and Zygosaccharomyces) this vegetative stage is the gametophyte.

The most recent investigations on the Ascomycetes and rusts indicate an undoubted alternation of generations in these groups. It

will certainly be interesting, therefore, if the yeasts can be shown to exhibit like phenomena, but apparently these forms need to be further investigated before alternation of generations can be regarded as firmly established.

From the above résumé it will be seen that the doctrine of the sexuality of the Ascomycetes has steadily advanced since DEBARY's time, but an immense number of forms remain yet to be investigated as to the initial stages of the ascocarp. While much investigation has centered on the sexual apparatus, the study of the development of the ascospores has by no means been neglected. Within recent years a considerable literature has been developed relating to the cytology of the ascus. We are concerned more especially with the method of spore formation and the phenomena of chromosome reduction, and the literature of this phase of the subject may be summarized as follows:

GJURASIN ('93) first observed mitoses in the ascus of *Peziza vesiculosa*, maintaining that the divisions are karyokinetic and that the prophases and anaphases take place inside the nuclear membrane. He discovered well-marked asters but describes no centrosomes. In the last or third division the spindles are placed at right angles to the length of the ascus. The asters of these nuclei persist for a remarkably long time, and the astral rays, although not connected with the nuclei, are folded back over them.

DANGEARD ('94) in studying very young asci of *Peziza vesiculosa* and *Borrera ciliaris* discovered the two primary nuclei of the ascus, which fuse to form the large ascus nucleus. Four nuclei appear in the recurved tip of a young ascogenous hypha. By means of transverse walls the nuclei are so separated that one remains in the end cell, two in the penultimate cell, and one in the antepenultimate cell. The ascus grows out from the penultimate cell and the two nuclei fuse to form the ascus nucleus. This according to DANGEARD is a true sexual union.

HARPER ('95, '96, '97 '99, :00, :05) has made the most thorough study of the structure and division of the nuclei in a number of Ascomycetes. He discovered and described the rôle of the kinoplasmic fibers in the formation of spores. He first counted the number of chromosomes in several species. In *Pyronema confluens* he also

observed that there are at first two nuclei in the recurved tip of an ascogenous hypha, which divide simultaneously by mitosis, thus forming four. One of each pair of nuclei enters the young ascus, which arises as an outgrowth of the penultimate cell. These two nuclei, which in this case are thus shown to be not sister nuclei, fuse to form the ascus nucleus. In a study of spore formation HARPER determined and fully described the process involved in the delimitation of the spores. Each nucleus forms a beak which is connected with a persistent central body, bearing at its outer end the astral rays. These rays bend backward and downward, finally coming in contact laterally and fusing to form a thin membrane, which continues to grow backward until a focal point is reached, thus completing the process of spore delimitation. This kinoplasmic membrane cuts the spore out of a homogeneous mass of protoplasm. He has described this process in *Erysiphe communis*, *Peziza vesiculosa*, *Ascobolus furfuraceus*, *Lachnea scutellata*, *Pyronema confluens*, and *Phyllactinia corylea*.

BERLESE ('99) has studied spore formation in *Tuber brumale*, concluding that the plasma membrane of the spore is formed from the astral rays. His results on nuclear phenomena agree essentially with those of GJURASIN and HARPER. MAIRE (:03, :04, :05) has described the nuclear divisions and ascus formation in *Galactinia succosa* and several other Ascomycetes, and confirms the method of spore formation as described by HARPER.

GUILLIERMOND (:03, :04, :05) studied several species with especial reference to karyokinetic division, the structure of the epiplasm, and the formation of the asci. He confirms the results of MAIRE on *Galactinia succosa*, finding that the tips of the ascogenous hyphae are not recurved, but that the terminal cells give rise to the asci. Wherever spore delimitation was studied it was found to follow the method described by HARPER.

BARKER (:03, :04) in a preliminary study of Ryparobius, a form whose asci contain more than eight spores, finds that the asci are formed from the penultimate cells of the ascogenous hyphae which contain two nuclei, these subsequently fusing to form the ascus nucleus. He also studied the nuclear divisions and spore formation. Sixty-four free nuclei are formed, which become regularly grouped

in the peripheral, dense, granular protoplasm of the ascus. Other series of divisions usually occur and uninucleate spores are eventually formed. The details of spore formation have not been described by BARKER. The description of spore formation in this many-spored form will be of great value, and BARKER's results will be awaited with interest. He is inclined to believe that the whole process of spore formation is intermediate between typical methods in sporangia and asci.

MAIRE (:**05**) concludes that in *Galactinia succosa*, *Pustularia vesiculosa*, *Rhytisma acerinum*, *Morchella esculenta*, *Anaptychia ciliaris*, and *Peltigera canina* the first division of the ascus nucleus is heterotypical, and that the second division is homeotypical. In the prophases of the first division he finds a well-marked synapsis stage. The asci are formed by two different processes, one of which is characterized by the formation of a hyphal system sympodially branched, each cell of which is a synkaryon containing two nuclei which divide by conjugate division. The binucleate terminal cells of these ascogenous hyphae become the asci. He believes that there is a tendency in the Ascomycetes to form a synkaryophyte analogous to that of the Basidiomycetes. MAIRE, however, has been unable to trace these synkaryons back to their first beginnings, which is highly important. In Galactinia the centrosomes and spindles have an intranuclear origin, while the polar asters have an extranuclear origin, developed independently of the intranuclear part. Nuclear beaks are formed in the process of spore delimitation.

GUILLIERMOND (:**05**) finds that in *Acetabula leucomelas* and in *Galactinia succosa* the ascogenous hyphae form a series of binucleate cells, the end cells of which become the asci. *Peziza catinus* presents still another method of ascus formation, which he holds to be analogous to that in *P. vesiculosa*. The terminal cells of the ascogenous hyphae are uninucleate, while the subterminal cells are binucleate. These binucleate subterminal cells bud out a lateral branch to form the ascus, which grows parallel to the filament, and in which nuclear fusion occurs to form the ascus nucleus. GUILLIERMOND has studied the behavior of the chromatin in the asci of *Pustularia vesiculosa*, *Peziza rutilans*, *P. catinus*, and *Galactinia succosa*, and believes that the first ascus mitosis is heterotypical, and that the first mitosis is preceded by a synapsis stage.

FAULL (:05) in a cytological study particularly of *Hydnobolites* sp., *Neotiella albocincta*, and *Sordaria fimicola* finds also numerous cases in which the ascus does not arise from the penultimate cell of the recurved tip of the ascogenous hypha, as originally described by DANGEARD. Such is invariably the case in only eleven out of the thirty-six species studied. In some species he claims that the asci bud out from the penultimate cells of the ascogenous hyphae, in others from the terminal cells, and in a few cases apparently from any cell. The uninucleate state of the ascus is preceded by a fusion of two nuclei, which may be sister nuclei. The centrosome and asters are extranuclear in origin, while the spindles are intranuclear. Enucleate portions of spores may be cut off, as in Podospora. FAULL's description of spore formation is particularly interesting, as it differs entirely from that described by HARPER. The spindle fibers elongate, bringing the daughter nuclei to the periphery of the sporeplasm, with their centrosomes in contact with the plasma membrane. The spores are delimited about each nucleus by the differentiation of a hyaline, finely granular protoplasm, which begins at the centrosome and finally entirely encloses the sporeplasm. The plasma membrane is subsequently formed from or in this hyaline area, and concurrently with this a second membrane is formed in contact with the first, lining the cavity in which the spore is to lie. FAULL suggests that the membrane may arise by a cleavage in the limiting area, caused by its growth and differentiation, together with a pull on the part of the nucleus. Both plasma membranes are intimately concerned in laying down the exospore. He can find no evidence that the astral rays fuse to form a membrane which cuts out the sporeplasm. FAULL also favors the view which homologizes the ascus with the zoosporangium of the Oomycetes, as an argument in favor of the origin of the Ascomycetes from the Oomycetes.

FAULL (:06) also concludes that the ascus of the Laboulbeniaceae contains a fusion nucleus which divides by three successive divisions. The process of spore formation is, as he states, essentially the same as he has described for other Ascomycetes.

In *Humaria granulata* BLACKMAN and FRASER (:06) find that the asci are usually developed from the subterminal cells of the recurved tips of the ascogenous hyphae. In two cases they found asci

developed from the terminal cells of these hyphae, as described by MAIRE for *Galactinia succosa*. These authors have not made a detailed study of the nuclear phenomena, but believe that spore formation is essentially the same as described by HARPER.

RAMLOW (:**06**) finds that the single ascus of *Thelebolus stercoreus* arises directly from the ascogonium, as in Spaerotheca. The two primary ascus nuclei fuse, and the resulting nucleus by successive divisions forms an enormous number of free nuclei. The details of karyokinesis have not been followed, although he satisfied himself that the divisions are indirect. The nuclei are evenly distributed in the ascus. The phenomena of spore formation were not accurately determined, but RAMLOW, basing his conclusions on the appearance of the protoplasm, which does not cleave as in the sporangium of the Phycomycetes, the appearance of an epiplasm, and the position of the nucleus at one end of the young spore, believes that the process of spore formation is by free cell formation, just as in Erysiphe.

THE NUMBER OF CHROMOSOMES RECORDED IN ASCOMYCETES.

Plant	Chromosome number	Observer	Year
Aleuria cerea	8	Guilliermond	1903, 1904, 1905
Anaptychia ciliaris	4	Dangeard	1903
Anaptychia ciliaris	8	Maire	1904, 1905
Anaptychia ciliaris	8	Guilliermond	1905
Ascobolus furfuraceus	8	Harper	1895
Ascobolus furfuraceus	4	Dangeard	1903
Ascodesmis nigricans	4	Dangeard	1903
Endocarpon miniatum	4	Dangeard	1903
Erysiphe communis	8	Harper	1900
Galactinia succosa	4	Maire	1903, 1904, 1905
Galactinia succosa	8	Guilliermond	1905
Hydnobolites sp	4 or 5	Faull	1905
Hypomyces Thiryanus	4	Maire	1905
Morchella esculenta	4	Dangeard	1903
Neotiella albocincta	6 or 7	Faull	1905
Otidea onotica	8	Guilliermond	1903, 1904
Peltigera canina	4	Maire	1904, 1905
Peziza catinus	12	Guilliermond	1903, 1904
Peziza catinus	16	Guilliermond	1905
Peziza rutilans	12	Guilliermond	1903
Peziza rutilans	16	Guilliermond	1904, 1905
Peziza Stevensoniana	8	Harper	1895
Phyllactinia corylea	8	Harper	1905
Pyronema confluens	10	Harper	1900
Pyronema confluens	4	Dangeard	1903
Pustularia vesiculosa	4	Maire	1904, 1905
Pustularia vesiculosa	8	Guilliermond	1905
Rhytisma acerinum	4	Maire	1904, 1905
Ryparobius sp	8 (?)	Barker	1904
Sphaerotheca castagnei	4	Dangeard	1903

The determination of the number of chromosomes in the ascus as well as in other cells is of the highest importance, as it will indicate the real nature of alternation of generations in the higher fungi. Since the chromosome number has been determined by several authors for a number of species of Ascomycetes, it may prove useful to summarize the results. (See the foregoing table.)

That there is considerable difference of opinion as to the chromosome number even in the same species of some Ascomycetes is evident from the above table. In Ascobolus and Pyronema HARPER finds eight and ten respectively; while DANGEARD claims that there are four in both species. GUILLIERMOND and MAIRE have established the number eight for Anaptychia; while DANGEARD claims four for this species also. MAIRE counts four chromosomes in *Galactinia succosa* and *Pustularia vesiculosa*, while GUILLIERMOND claims that there are eight in each of these forms.

From the above résumé it seems perfectly evident that no such hypothesis as that the chromosome number four is general among the Ascomycetes, as DANGEARD imagines, can be maintained. In this group, on the contrary, judging from the above facts, related species may vary in their respective chromosome numbers, just as has been found to be the case in many of the higher plants.

In a recent paper MAIRE (:**05**) criticizes GUILLIERMOND (:**05**) for saying that he maintains that there are probably four chromosomes in all Ascomycetes, but admits that he and DANGEARD have formulated practically parallel hypotheses on this point. DANGEARD (:**03**), however, distinctly refers this hypothesis to MAIRE (Séance de la société mycologique de France tenue à Poitiers en Octobre, 1903), and says "Cette découverte a été faites simultanément et d'une manière indépendante par MAIRE et nous: elle offre, semble-t-il, toutes garanties de certitude." It appears from these facts that MAIRE has the responsibility of having first made the claim made by DANGEARD, but which MAIRE now attributes to him. It is perfectly plain that no basis for such a hypothesis exists, a fact which MAIRE apparently fully recognizes.

Since DANGEARD first described the asci in a number of forms as arising from the cell next the terminal one, several deviations from this type have been reported. That no such regular process of ascus

formation obtains in general in the whole group of Ascomycetes, or even in nearly related genera, is clearly evident from a study of the more recent cytological investigations, especially those of MAIRE, GUILLIERMOND, and FAULL. In the following résumé no pretense of absolute completeness is made.

We may note first those very simple forms which have sometimes been classed together as Hemiasci, though in most cases, as KUYPER shows, the types are plainly not closely related. The genera Ascoidea (POPTA '99), Protomyces (SAPPIN-TROUFFY '97, POPTA '99), and Taphridium (JUEL :02) possess a septate mycelium with multinucleate cells, from which the sporangia arise directly without the intervention of sexual organs. The hyphal cells of Protascus (DANGEARD :03) also give rise directly to the asci. Sexual organs are present in Dipodascus (JUEL :02) and Eremascus (EIDAM '83), and the fertilized oogonium forms a single ascus. Monascus (BARKER :03, OLIVE :05) apparently forms a branched ascogenous hyphal system, each cell of which is able to produce an ascus. The heterogeneity of these forms is evident by the fact that the asci arise directly from an oogonium, from hyphal cells, or from the cells of ascogenous hyphae.

In some yeasts the conidia become transformed immediately after nuclear fusion into so-called asci, as in Schizosaccharomyces and Zygosaccharomyces, while in others the conidium is transformed directly into the ascus and fusion comes later, as in *S. Ludwigii* (GUILLIERMOND :05).

In the Exoasci the binucleate cells of the mycelium are transformed immediately into a single ascus, as in *Exoascus deformans* (DANGEARD '94) and Taphrina (SADEBECK '93, IKENO :01, :03). Among the Gymnoascaceae, *G. Reesii* and *G. candidus* (BARANETZKY '72, EIDAM '83, DALE :03) have their asci arising from the end cells of a series of short ascogenous hyphae. If CLAUSSEN'S (:05) Boudiera is really *Ascodesmis nigricans*, as CAVARA (:05) believes, and if Ascodesmis belongs among the Gymnoascaceae, then we have a form in this group whose asci arise from the penultimate cells of the recurved tips of the ascogenous hyphae.

The Perisporiaceae show considerable variation in the method of ascus formation. The early works of DEBARY and others may be

passed over, as the methods used by them were not sufficiently delicate to enable them to determine the exact method of ascus formation. The end cells of ascogenous hyphae described by DEBARY for Eurotium, for example, may as well represent subterminal cells. In the mildew, *Erysiphe communis* (HARPER '96), the end cells of the ascogenous hyphae may develop the asci. This is also the case in *Phyllactinia corylea* (HARPER :05), but asci may also be formed as lateral branches of intercalary cells. In *Sphaerotheca castagnei* (HARPER '95) and *S. humuli* (BLACKMAN and FRASER :05) the oogonium develops into an ascogonium of five or six cells, of which the penultimate one grows into a single ascus. In this genus there are no ascogenous hyphae, unless we accept the interpretation of BLACKMAN and FRASER that the ascogonium is a single ascogenous hypha, whose penultimate cell develops an ascus in the manner described by DANGEARD. In *Anixia spadicea* (FAULL :05) the asci spring from any cell of the ascogenous hyphal system.

In the Tuberaceae, *T. melanospermum* (DANGEARD '94, GUILLIERMOND :04) has its asci arising as described by DANGEARD; while *Genea hispidula* (FAULL :05) shows a marked variation from this type. In this form the ascus grows out from a curved terminal cell. FAULL suggests that perhaps the only difference between this and the other type is the lack of a cross wall cutting off the uninucleate hyphal tip.

Among the apogamous Pyrenomycetes, such as *Teichospora trimorpha*, *T. aspera*, *T. nitida*, and *Teichosporella* sp. (Miss NICHOLS '96), a uninucleate ascus arises from a single central cell of the perithecial mass. *Hypomyces Thiryanus* (MAIRE :05) follows the method described by DANGEARD; while in *Podospora ascerina*, *P. setosa*, *Sordaria fimicola*, and *S. humana* (FAULL :05) the asci arise from a curved terminal cell of an ascogenous hypha. In *Phyllachora graminis* (FAULL :05) the ascus arises from a curved cell of the tip without the formation of a uninucleate tip-cell.

The Discomycetes are described as showing the greatest uniformity in the method of ascus formation, which may perhaps be due to the fact that more careful work has been done upon them. All the following forms have their asci formed in the manner described by DANGEARD ('94) for *Peziza vesiculosa*: *Borrera ciliaris*, *Acetabula*

calyx (DANGEARD '94), *Peziza Stevensoniana*, *Ascobolus furfuraceus* (HARPER '95), *Lachnea scutellata*, *Pyronema confluens* (HARPER :00), *Aleuria cerea* (GUILLIERMOND :03, :04), *A. amplissima*, and *A. olivea* (GUILLIERMOND :04), *Peziza catinus*, *P. venosa*, *P. rutilans* (GUILLIERMOND :04), *Ascobolus marginatus*, *Otidea onotica* (GUILLIERMOND :03, :04), *Acetabula vulgaris*, *Pyronema confluens*, *Ciboria echinophila*, *Bulgaria inquinans*, *Guilliermondia saccabaloides* (GUILLIERMOND :04), *Peziza* sp. (FAULL :05), *Ryparobius* sp. (BARKER :03, :04), *Neotiella albocincta*, *Acetabula* sp., *Pseudoplectania* sp., (FAULL :05), *Boudiera Clausseni* (CLAUSSEN :05), *Peziza vesiculosa* (MAIRE :05), *Thelebolus stercoreus* (RAMLOW :06), *Humaria granulata* (BLACKMAN and FRASER :06), *Thecotheus Pelletieri* (OVERTON :06). Several variations from the type described above also occur among the Discomycetes. *Galactinia succosa* (MAIRE :03, :05, GUILLIERMOND: 03, :05), *Acetabula leucomelas* (GUILLIERMOND :03, :04, :05), *Acetabula vulgaris* (MAIRE :03) have their asci arising from binucleate terminal cells. GUILLIERMOND (:03) also found that *Pustularia vesiculosa* occasionally has its asci arising in a like manner. *Peziza catinus* and *P. vesiculosa* (GUILLIERMOND :05) occasionally have the asci arising from the subterminal cells of the ascogenous hyphae whose tips are recurved. *Acetabula acetabulum* (GUILLIERMOND :03) has binucleate cells formed in the curved tips of the ascogenous hyphae which do not form the asci, but give birth to a series of two, three, and four cells, of which the terminal ones produce the asci. In *Discina venosa* (FAULL :05) the ascus arises from a curved terminal cell. In *Urnula craterium* (FAULL :05) the ascus may spring apparently from any cell whatever. In *Humaria granulata* (BLACKMAN and FRASER :06) the ascus occasionally arises from the terminal cell.

A number of the Helvellaceae have been studied, which also show great variation in the mode of ascus formation. *Helvella ephippium* (DANGEARD '94), *Morchella esculenta* (DANGEARD '94), *Helvella sulcata*, *H. elastica*, *H. crispa* (GUILLIERMOND :04), *Morchella esculenta*, *M. conica*, *Helvella astra*, *H. lacunosa*, *H. elastica* (FAULL :05) have their asci formed from the penultimate cells of the recurved tips of the ascogenous hyphae, in the manner described by DANGEARD for Morchella. In *Geoglossum ophioglossoides*, *G. hir-*

sutum, Geoglossum sp., *Verpa conica, Gyromytra sphaerospora, Leptoglossum luteum, Leptoglossum* sp., *Mitrula phalloides, Leotia lubrica, L. chlorocephala* (FAULL :05) the ascus grows out from the terminal cell, and no uninucleate end cell is cut off. In *Verpa bohemica* (FAULL :05) is found the very greatest variability; the asci appearing as outgrowths of a terminal cell, or from a second, third, or even fourth cell from the tip.

The lichens *Anaptychia ciliaris* (DANGEARD :03), and *Peltigera canina* (MAIRE :05) have their asci regularly formed according to DANGEARD'S method; but *Anaptychia ciliaris* (MAIRE :05) apparently develops its asci from the subterminal cells of the ascogenous hyphae, while the tips, according to MAIRE, may continue development. BAUR (:01, :04), although he does not describe the method of ascus formation, figures ascogenous hyphae which are recurved in *Pertusaria communis.*

In the foregoing I have endeavored to group our knowledge of the various methods of ascus formation according to the natural classification of the forms investigated, in order that the significance of the variation described may be more apparent. It is the nuclear history which is theoretically most interesting, and is thus most essential to determine the relative ancestry of each of the nuclei which fuse in the ascus. This has been done for very few forms as yet. In Pyronema, HARPER (:00) has been able to trace the origin of the two primary nuclei of the ascus, in a case in which the tips of the ascogenous hyphae at first contain two nuclei. These divide by simultaneous division. Of the four nuclei thus formed, one lies in the terminal cell, and two, which are not sister nuclei, in the subterminal cell which becomes the ascus.

Thecotheus belongs to that group of the Discomycetes (Ascobolaceae) whose small fruit bodies are nearly always found growing freely on dung. The species in question occurs on horse dung. It was found on cultures which were old and partly dried up in the Botanical Laboratory of the University of Wisconsin. These cultures were kept running, yielding an abundant supply of material during the progress of this investigation. The fungus has since been found free in nature. The apothecia are very small, about 0.5^{mm} in diameter and 0.25^{mm} high, of a white or yellowish color. When

wet they are therefore plainly visible to the naked eye. A distinct thin excipulum, or lateral boundary of vegetative hyphae, surrounds the hymenium (*fig. 3*). This excipulum is densely covered with short, blunt ends of protruding vegetative hyphae, which give a hairy or warty appearance to its surface. The sterile tissue of the secondary mycelium extends outward and downward to form a pseudo-parenchymatous skirt-like structure, which also extends along the substratum beneath the hypothecium. This lower layer becomes adjusted to the irregularities of the substratum, from which numerous hyphae enter the fructification. The equilibrium of the whole fruit body is maintained by means of this much broadened pseudo-parenchymatous base (*fig. 3*).

The apothecia are at first globular or cylindrical, later becoming broadened, discoid, and somewhat biscuit-shaped (*fig. 2*). The asci are roughly cylindrical in form, about $220\times35\mu$, their greatest diameter being near the top. Each ascus contains thirty-two ellipsoidal, slightly colored spores, each about $17.5\times28\mu$, which are discharged through a small terminal pore. This pore is at first covered by a small cap or operculum, bounded by a thickened ring in the wall of the ascus where the cover breaks off (*fig. 16*). The asci develop from the subhymenium successively; each fruit body thus contains asci and spores in all stages of development. Numerous long and slender septate paraphyses, about 360μ long, arising from the hypothecium, are thickly packed among the asci. At the surface each paraphysis has a somewhat swollen protruding tip (*figs. 2, 3*). The mature spore contains a single nucleus in a mass of very densely granular protoplasm (*fig. 15*). The thin, very pale exospore is corrugated on its outer surface, much like many other spores of the Ascobolaceae. There is a passage through this exospore at each end, as well as through the thick hyaline endospore, to form what is apparently a terminal germinal pore. The spores are not shot out of the asci, but appear to be squeezed out by turgor, together with the lateral pressure exerted by the turgor of the neighboring asci and paraphyses. They are to be found as a dust on the surface of the apothecium, often adhering in masses. Possibly in consequence of the smallness of the terminal aperture of the ascus the spores are not projected or discharged violently. This condition is not general

among other forms of the Ascobolaceae, in most of which the spores are projected for some distance through the terminal pore of the ascus.

Modifications of the usual strengths of Flemming's chromacetic osmium fixing fluids were exclusively used in the preparation of the material. Portions of the substratum upon which apothecia grew were removed and dropped into the fluids. Beside the mature fruits many younger stages were thus obtained. The sections were stained with safranin gentian-violet orange-G combinations and also with Heidenhain's iron-alum haematoxylin. The sections were cut 5–10 μ thick.

HARPER ('95, '96, :05) has shown that the ascogonia of the mildews consists of a much curved row of cells, each of which contains a single nucleus, with the exception of the penultimate cell, which contains two or several nuclei, and which forms the ascus in Sphaerotheca, out of which grow the ascogenous hyphae in other forms. BARKER (:03, :04) also observed the same kind of ascogonium in Ryparobius; while CLAUSSEN (:05) finds several such ascogonia in Boudiera. The youngest ascogonium which I have thus far observed in Thecotheus consisted of a row of several cells which were already multinucleate (*fig. 1*). HARPER ('96) figures and describes perforations in the cross walls in the ascogonium of Ascobolus connecting the adjacent cells. One of the cells of the row is larger. It is from this particular cell that the ascogenous hyphae arise, and out of which the nuclei enter the ascogenous hyphae from it and the neighboring cells. As soon as the ascogonia become empty they undergo disintegration. BARKER (:04) finds each cell of the row in Ryparobius at first uninucleate and then binucleate or occasionally quadrinucleate. From the cells of the row the ascoge ous hyphae delevop. He does not distinctly say that they develop from any particular cell of the ascogonium. CLAUSSEN (:05) finds that the gametes of Boudiera contain several nuclei, which however fuse in pairs in the oogonium. Several walls are formed, so that the resulting ascogonium consists of a row of several cells from which the ascogenous hyphae arise. Thecotheus agrees with Ryparobius and Boudiera in that the ascogenous hyphae do not arise from any single cell of the ascogonium, but from any or all of them (*figs. 1* and *2*). The youngest ascogonia which I have been able to find were

already multinucleate, some containing as many as a dozen nuclei, each much larger than those of the vegetative cells. *Fig. 1* shows a young fruit body with sections of several ascogonia, each of whose cells are multinucleate. No connections between the adjacent cells could be observed.

Unlike Ryparobius and like Boudiera, Thecotheus has a compound fruit body. *Fig. 1* represents a section of a young ascocarp, in which several ascogonia are present. One ascogonium, composed of several multinucleate cells, is shown, which resembles in shape the ascogonium of Ascobolus. In the same section, surrounded by the same investment of vegetative hyphae, may be seen also sections of several other ascogonia. These ascogonia are always closely interwoven, so that they are cut in different planes. Other views of the same ascogonia appear in adjacent sections of this ascocarp.

Concurrently with the development of ascogenous hyphae, investing vegetative hyphae encircle the ascogonia, the young ascogenous hyphae, and the asci. This condition can be seen in *fig. 2*. Remnants of the ascogonia are still plainly visible, and the branching ascogenous hyphae can be seen to contain several nuclei, each with a single nucleolus. The nuclei of the ascogenous hyphae are from three to four times as large as those of the paraphyses, making them therefore easily distinguishable. Each cell of the vegetative tissue contains several nuclei. I have been unable to find any regular series of binucleate cells.

The developing ascogenous hyphae are profusely branched, pursuing such irregular paths that it is impossible to follow their course for any great distance. Transverse longitudinal and oblique sections appear in the preparations, which are only mere fragments of the whole system (*fig. 2*). From *fig. 2*, however, it is plain that the ascogenous hyphae develop considerably before transverse septa are put in. The nuclei are especially abundant near the tips of the branches. At the time the cell division is complete, the tips of the branches of the ascogenous hyphae are bent backward as they push upward among other branches and paraphyses. The terminal cell is uninucleate, while the subterminal cell is binucleate. The nuclei of these branches can be seen to be considerably larger than those of the ascogonium (*fig. 4*). From these binucleate subterminal cells

the asci develop. So far as I have been able to observe, asci were never developed from the terminal cell, or from the third cell from the tip, although either condition may possibly occur. Thecotheus certainly does not contain a system of ascogenous hyphae, each cell of which is a synkaryon, as described for Galactinia and *Pustularia vesiculosa*.

In Thecotheus the subterminal cell of an ascogenous hypha arches up to form the young ascus. The two nuclei apparently fuse to form the ascus nucleus (*fig. 4*). The young club-shaped ascus is filled with a dense finely granular vacuolated protoplasm, in which are situated numerous deeply staining extranuclear granules, probably the metachromatic granules of GUILLIERMOND (:**03**), which have also been observed and described by other authors. The fusion nucleus greatly enlarges as the ascus grows, thus maintaining a definite nucleo-cytoplasmic relationship, as described by HARPER (:**05**). Within the nucleus chromatic filaments are organized, which give the appearance of a loose spirem. Division stages were not observed, but, so far as I have been able to find, the nuclear structures are essentially the same as have already been many times described.

The young ascus, which elongates rapidly, crowding up into the hymenium, is somewhat broadened at its tip, gradually narrowing toward the base. The protoplasm, packed in the tip, is coarse and granular (*fig. 7*). A spore region is organized about the nucleus. A large region, in which the protoplasm is very foamy, is present both above and below the central denser sporeplasm. The ascus increases still more in size, the denser regions at the apex and about the nucleus becoming still more sharply separated by the large vacuolated space (*fig. 8*). A peripheral layer of denser protoplasm connects the apical and central regions. The distinction of central and apical regions and the two large vacuolated spaces with foamy protoplasm persist throughout the process of spore formation (*figs. 8–12*). The primary ascus nucleus divides rapidly by three successive divisions to form eight free nuclei. During these divisions there is a gradual decrease in the size of the nuclei, as has also been observed in other asci. In *fig. 10* it will be seen that each of the eight nuclei are very small compared with the nuclei represented in *figs. 7* and *8*. From the abundant stages found in the conditions represented in *fig. 10*, I am

inclined to believe that there is a pause before further divisions occur and a growth period of these eight nuclei. Not only do the nuclei increase in size before dividing, but the asci also lengthen very much and the protoplasm becomes still more vacuolated and foamy (*fig. 11*). Perhaps this increase in size of the nuclei is also correlated with the increase in the amount of cytoplasm in the ascus. Eventually each of these eight nuclei divides to give sixteen free nuclei, no spores being yet delimited (*fig. 11*). In *fig. 11* each nucleus is about as large as one of the daughter nuclei in *fig. 8*. These nuclei certainly show a marked increase in size over those of *fig. 10*. It will also be observed that the nuclei are irregularly arranged in the central region of the sporeplasm. Each of these sixteen nuclei undergoes still another division, resulting in thirty-two free nuclei being found in the ascus. No figure representing this thirty-two nucleate stage has been drawn, although the nuclei were seen in the preparations. *Fig. 6* represents a portion of such a stage. The nuclei here are also very much smaller than in *fig. 11*.

In Ryparobius BARKER (:**03**, :**04**) finds that the number and size of the spores vary in different asci. More than two hundred were normally found in a single ascus, but as few as sixteen have been seen. In Ryparobius successive nuclear divisions occur rapidly, until sixty-four free nuclei are formed. These become regularly grouped in a dense granular mass of protoplasm around the periphery of the ascus. Other series of divisions now usually occur, and eventually uninucleate spores are formed. In Thelebolus (RAMLOW :**06**) many nuclei arise in the ascus, about each of which a spore is delimited, as described by HARPER.

In Thecotheus the spores are delimited from the homogeneous central portion of the cytoplasm immediately after the formation of the thirty-two nuclei. So far as I have been able to observe, the entire process of spore delimitation is accomplished by means of the kinoplasmic fibers which form the astral radiations of the central body. The nucleus becomes pointed or beaked, bearing a central body at its outer end, from which the kinoplasmic radiations extend (*fig. 6*). The chromatin lies freely in the nuclear cavity, apparently connected with the central body. The process of spore delimitation is apparently precisely like that described by HARPER for *Erysiphe communis*,

Lachnea scutellata, *Pyronema confluens*, and *Phyllactinia corylea*. As soon as the beak has reached a certain length, which is comparatively short in Thecotheus, these kinoplasmic fibers bend downward and grow backward over the nucleus, fusing laterally to form a continuous plasma membrane, which separates the cytoplasm of the spore from that of the epiplasm. The nuclear beak is withdrawn and a somewhat pointed nucleus remains in the young spore (*fig. 6*), which gradually resumes the spherical shape of a resting nucleus. Although the process of spore delimitation is not easily followed in Thecotheus, I am convinced that it is essentially the same as HARPER has described for other Ascomycetes. I have also had an opportunity to compare my own preparations containing this stage with those of HARPER on Erysiphe and Lachnea, which objects he found most favorable for study. I can see no essential differences in appearances. The nuclear beaks do not have any special orientation or relation to the plasma membrane, as has been figured and described by certain authors for other forms. The beaks may lie at any angle during the process of spore delimitation.

BARKER (:04) believes the process of spore formation in the many-spored asci of Ryparobius to be unlike that in the typical ascus. "The protoplasm passes through a series of characteristic changes during the development of the ascus, and the whole process of spore formation seems to be intermediate between typical methods in sporangia and asci." We shall await BARKER'S completed account of the spore formation in this form with great interest. We have seen that the method of spore delimitation in the many-spored asci of Thecotheus is exactly similar to that found in typical eight-spored asci. As noted in another connection, FAULL entirely dissents from the method of spore formation as described by HARPER. I have been unable to discover in Thecotheus the presence of hyaline zones in connection with which cleavage takes place to delimit the sporeplasm from the epiplasm as described by FAULL, and I am certain that no such method of spore formation exists in Thecotheus.

Fig. 6 represents a spore in the process of delimitation as described above. In the same figure a very young spore is also shown, which has its delimiting membrane already formed and the nuclear beak withdrawn. It will be observed that the sporeplasm is nearly like

the surrounding epiplasm, perhaps slightly more dense and granular. No particular granular area is present. It is simply a portion carved out of the homogeneous cytoplasm in which the nucleus is situated by means of a delimiting kinoplasmic membrane. In *figs. 12a–12c* slightly older spores are shown. They are arranged in the form of a hollow cylinder around the wall of the ascus. About five young spores are arranged vertically along the ascus walls in any one plane. *Fig. 12a* represents a median longitudinal section of the ascus; *figs. 12a* and *12b* are slices off the same ascus.

BARKER (:**03**) found that the numerous nuclei in the asci of Ryparobius became arranged in the form of a hollow sphere just beneath the wall of the ascus before spore delimitation. Each ascospore when completely formed, therefore, has one end toward the center and the other toward the ascus wall, the resulting arrangement of the spores thus being radial. In Thecotheus the nuclei, as noted above, are not arranged radially, but in the form of a hollow cylinder about the wall of the ascus, in a denser peripheral layer of the epiplasm. The resulting spores, therefore, have their long axes parallel to the wall of the ascus. In this respect Ryparobius and Thecotheus are essentially different. Due to this peripheral arrangement into a hollow cylinder, the spores are forced to occupy considerable space in the ascus, some being pushed up near the tip. The epiplasm is at this time everywhere much more vacuolated than in earlier stages, and the ascus is exceedingly turgid and swollen (*figs. 12a–12c.*)

In *fig. 12a* the spores can be seen to show no sign of an exospore or endospore. DEBARY ('**63**, '**64**) thought that the exospore was laid down upon the surface of the spore from the epiplasm, which explanation seems to have gained rather widespread acceptance. The exact method of exospore formation needs investigation. FAULL (:**05**) believes that two membranes are formed, one being the plasma-membrane of the spore and another formed concurrently with this, which lines the cavity in which the spore is to lie. These membranes occupy the position of the hyaline zone described above. The spore wall is supposed to be laid down between the membrane bounding the epiplasm and the plasma membrane of the spore. FAULL suggests that both membranes are perhaps active in the formation of the spore coats.

According to my own observations, the process of the formation of the spore coats does not agree with the account of FAULL (:05) *Fig. 13* shows a young spore which has grown somewhat beyond those found in *figs. 12a–12c*. The limiting membrane is not perceptibly thickened, showing in sections as an even unbroken line. Just inside this membrane, however, the endospore is seen to be but slightly differentiated from the sporeplasm, being much less vacuolated but more hyaline and granular. A more or less distinct boundary is present between the endospore and the sporeplasm. Exactly how the endospore is formed I am at present unable to state, unless it is laid down by the original plasma membrane, which has gradually withdrawn, secreting the substance of the spore coats as it recedes. Finally, the endospore becomes still more granular and hyaline as the spore develops (*fig. 14*). The outermost portion of the hyaline granular area constitutes the exospore. In *fig. 14*, which is not so highly magnified as *fig. 13*, the central portion of the sporeplasm is highly vacuolated. The nucleus of the spore lies in the center of this mass of protoplasm. The irregularities on the exospore may be due to fixation. Lines are developed on the surface of the spore, finally producing an irregularly branched system of elevations and ridges much like that found on the spores Ascobolus. *Fig. 15* represents a mature spore. The two germinal pores, one at either end, are present, passing through the spore coats. The mature endospore is very granular and highly refractive. The inner protoplasm, bounded by the plasma membrane, is still uninucleate but densely granular. Smaller vacuoles have entirely disappeared. In some mature spores two large spherical oil drops are present, one at either side of the nucleus, but not regularly so. *Fig. 15* is typical.

As the asci dry out, the walls become thickened and hyaline. *Fig. 16* shows the upper portion of a nearly mature ascus, at the apex of which is the cap or operculum in the process of formation. A thickened ring in the ascus wall is formed below the operculum. The mature spores are probably discharged through this terminal pore by the turgor of the ascus and the lateral pressure of other asci and paraphyses. Although several attempts were made to germinate these spores in various sorts of media, I have thus far been unsuccessful. Perhaps it may be necessary for them to pass through an ali-

mentary tract or to be naturally or artificially partly digested before germination will occur, or perhaps the spores tested may not have been mature.

I have shown that ascogonia are present from which the asci arise, although I have been unable to find the earliest stages of these organs in Thecotheus. Since in the forms in which sexual organs do exist, as described by several investigators, an ascogonium arises as the result of nuclear and cell divisions from a fertilized oogonium, I think it practically certain that such oogonia exist in Thecotheus. Since the ascogonia are in groups, several being present in each young ascocarp, it is also safe to conclude that the fruit bodies arise as the product of multiple sex organs, just as in Pyronema and Boudiera. Thecotheus, therefore, is another example of a form among the Ascobolaceae with a compound apothecium.

In Thecotheus the asci are developed from the penultimate cells of the recurved tips of the ascogenous hyphae, and they are at first binucleate, later becoming uninucleate in the usual manner. There is apparently no tendency here toward the condition described by MAIRE and GUILLIERMOND, wherein a system of binucleate cells are formed, as in Galactinia, corresponding to the synkaryophyte in which a long series of binucleate cells occur, the nuclei finally fusing in the basidium, as in the Basidiomycetes and rusts. MAIRE claims to have found that these binucleate cells of the ascogenous hyphae originate from hyphae of the subhymenium, whose cells are multinucleate. The first cell arising from these subhymenial hyphae contains two nuclei, which divide by a conjugate division, giving rise to a series of branching synkaryophytic hyphae, which eventually form the asci. This branched, ascogenous hyphal system MAIRE compares to the hyphal system which gives rise to the basidia in the Basidiomycetes. Although MAIRE and GUILLIERMOND have found this system of ascogenous hyphae in certain forms, it still remains and is of the highest importance to determine how the ascocarps originate in these forms. If, as HARPER (:05) suggests, the condition found in Pyronema, and still more advanced in Galactinia and *Pustularia vesiculosa*, could work back until the egg cell was reached, an apogamous condition might result, such as is now found in the Hymenomycetes (Miss NICHOLS :04), and the nuclear fusion in the ascus

might have acquired secondarily a sexual significance. Thecotheus with its ascogonia, and presumably also still earlier oogonia, shows no tendency towards this condition. I have been unable to find binucleate cells either in the paraphyses, in the mycelium, or in any of the vegetative cells of this fungus, and am sure that Thecotheus does not possess anything comparable to the synkarophyte of the Basidiomycetes.

The main problem relating to the asci at present is whether they are merely eight-spored sporangia or spore mother cells corresponding to those of the higher plants, and on this point the method of spore formation in a polysporous ascus should throw much light. As noted previously, I have confined my attention principally to Thecotheus on account of the abundance of this apparently very favorable form. The possibility that such asci might show transitional conditions leading over to those found in the sporangia of the lower fungi is very suggestive, and, as noted above, BARKER believes that in the asci of the nearly related genus Ryparobius he has found such transitional forms, although RAMLOW believes the ascus of Thelebolus shows no such sporangial characters. The distinction between typical sporangia and typical asci seems to be sharply drawn. In the sporangia of Sporodinia and Pilobolus HARPER ('99) has found that spore formation is by a process of progressive cleavage by means of furrows, either from the surface of the protoplasm or from vacuoles of the mother cell. The nuclei during the cleavage are in a resting stage and are not concerned in the process. Thus the formation of an epiplasm is precluded. HARPER has described the process of cell formation in *Synchitrium decipiens*, *Pilobolus crystallinus*, and *Sporodinia grandis;* while SWINGLE (:03) has observed the same process in the sporangia of *Rhizopus nigricans* and *Phycomyces nitens*. HARPER has pointed out that this process is not one of free cell formation in the sense in which the term is used for free cell formation in the ascus, in which the cells lie free in the mother cell included in the so-called epiplasm. He also concludes that these two very divergent methods of cell formation in asci and sporangia make it impossible to assume any close relationship between these two structures, and this difference is thus made an argument against the homology of the sporangium of the Phycomycetes and the ascus of the Ascomycetes.

Although attempts have recently been made to discredit HARPER'S results on the method of free cell formation in the ascus, no very convincing evidence has been brought forward to show that it is more like that in the sporangium. JUEL (:02) in his work on Taphridium seems to think that HARPER has placed too much stress on the action of the kinoplasmic fibers as one of the chief distinguishing characteristics of the process, saying: "Vorlaüfig können wir nicht die Rolle des Kinoplasmas bei der Zellbildung zur *nota characteristica* der freien Zellbildung machen, sondern müssen diesen Begriff in der herrkömmlichen Weise auffassen." Apparently JUEL has failed to comprehend the essence of HARPER'S definition.

FAULL (:05) does not believe that the methods of spore formation in the ascus and sporangium are so different as to prevent assumption of their homology. He favors the view that homologizes the ascus with the zoosporangium of the Oomycetes, as an argument in favor of the origin of the Ascomycetes from the Oomycetes. The most complete account of cell formation in the zoosporangia of the Oomycetes is that given for Saprolegnia and Achlya, although the behavior of the nuclei has not been thoroughly enough studied.

The earliest workers in the study of spore formation were influenced by their *a priori* views on the cell theory as a whole, and NÄGELI used it to support his doctrine that new cells are regularly formed by so-called free cell formation from old ones. PRINGSHEIM ('51) believed that spores were formed by simultaneous and not by successive bipartitions of the protoplasm, being completely bounded off before the appearance of a cellulose wall. BÜSGEN ('82) in his description of spore formation in the sporangium of the Phycomycetes believed that cleavage is due to a simultaneous formation of cell plates, which break down, being later formed again to separate the spores. BERTHOLD ('86) studied oogonia, but assumed that the process in oogonia and sporangia are alike. The peripheral layer of protoplasm which surrounds the central vacuole forms dense rounded masses about definite centers, which constantly increase in size, protruding gradually into the central vacuole. Finally the masses separate and round up, later swelling up so as to become pressed together and flattened. Finally these masses again round up, forming definite eggs or swarm spores. BERTHOLD claims that the position of the spores is predetermined by

centers of attraction, about which the protoplasmic lining of the walls is collected. The whole process is a form of free cell formation, in which the entire protoplasm is utilized, without involving the formation of a periplasm. He holds, therefore, that the sporangium of the Saprolegniaceae represents an advance over forms in which periplasm is formed. The sporangium is differentiated into central vacuole and peripheral protoplasm, and is perhaps a stratified structure in itself, whose polarity is determined by the position of the nuclei, which in turn influence the position of the spores, as has been pointed out by HARPER ('99).

According to the work of ROTHERT ('88), HARTOG ('88), HUMPHREY ('92), TROW ('95), and DAVIS (:03), the sporangium is multinucleate when cut off, the nuclei lying scattered in the peripheral layer of protoplasm. DAVIS practically confirms the account of the earlier authors. The uninucleate spores originate by means of clefts, which proceed from the central vacuole of the sporangium to the periphery, dividing the protoplasm into polygonal areas. The spores are later formed from these uninucleate areas. There is no mitotic division of the nuclei or cytoplasmic centers (coenocentra) in the zoosporangia.

HUMPHREY ('92) first studied oogenesis in Saprolegnia by means of modern technique, but was soon followed by TROW ('95, '99) and HARTOG ('95, '96, '99). There seems to be a great diversity of opinion as to the behavior of the nuclei, which far exceed the ultimate number used in the formation of eggs. HUMPHREY and HARTOG believe that the nuclei fuse in groups to form the functional nuclei. TROW claims that many nuclei degenerate until the requisite number is reached, which results DAVIS (:03) has confirmed, but differs from TROW in regard to the sexuality of the Saprolegniaceae. The oogonium arises as an enlargement of the end of a hypha, into which passes a dense mass of cytoplasm and nuclei. A central vacuole is formed, with a peripheral layer of protoplasm lining the walls in which lie the nuclei. The nuclei divide once by mitosis. The protoplasm aggregates into masses which form the eggs. The process of separating these masses by means of a series of fusing vacuoles, has been described by DAVIS. He finds that the egg initials are formed about cytoplasmic centers (coenocentra), much as has been described

for certain Peronosporaceae. It seems apparent that, even if we accept FAULL's description of spore formation in the ascus, the data are quite insufficient to support any view which homologizes the ascus with the zoosporangium or oosporangium of the Oomycetes.

BARKER (:**04**) announces that the protoplasm in the developing ascus of Ryparobius shows a series of changes in spore formation, which appear to be intermediate between typical methods in sporangia and asci. The account is only preliminary and has been referred to above. My own studies on the asci of Thecotheus however, have shown the process of spore formation to be as in other typical asci, namely, by means of the kinoplasmic radiations of the nucleus. Although more than eight spores are formed in the ascus, the process of spore delimitation is that found in a typical ascus. There is absolutely no evidence that the process is in the least similar to spore formation as found in the sporangia of the Oomycetes or in those of the Phycomycetes. The results obtained do not seem to throw the least light on the homology or origin of this peculiar organ. It apparently makes no difference whether less than eight spores are formed or more than eight, the phenomena of spore delimitation are exactly the same as found in typical eight-spored asci.

That a true alternation of generations, comparable to that found in the higher plants, exists among the Ascomycetes, is certainly obvious from the fact that the asci eventually arise as the result of fertilization. DEBARY ('**70**) advanced the opinion that the ascus fruit represents an asexual generation, and WORONIN ('**70**) compared it to the sporogonium of the moss, which idea was farther emphasized by HARPER ('**96**) for Erysiphe. The only essential difference is that the egg is never separated from the parental tissue system, agreeing in this respect with that of the red algae. HARPER also pointed out that the ascus is an analogue of the spore mother cell of the higher plants, and that the triple division corresponds to the double division in the spore mother cells of the higher plants, with a probable consequent chromosome reduction in the ascus. This view is further supported by the recent discoveries of MAIRE (:**05**), HARPER (:**05**), and GUILLIERMOND (:**05**) on the nuclear phenomena in the ascus, by which reduction of the number of chromosomes and a consequent return to the gametophyte generally occur. These authors have found

that the first division of the ascus nucleus is preceded by a well-marked synapsis phase, which the most recent zoological and botanical investigations have shown to be the most characteristic and important phase of the heterotypical division. While MAIRE finds a synapsis similar to that described by STRASBURGER (:04), HARPER and GUILLIERMOND have found the phenomena to be essentially the same as in the pollen mother cells of the flowering plants studied by GRÉGOIRE (:04), BERGHS (:04, :05), ALLEN (:04, :05), ROSENBERG (:05), STRASBURGER (:05), MIYAKI (:05), OVERTON (:05), TISCHLER, (:06), and CARDIFF (:06). HARPER finds permanent central bodies in the nuclei of Phyllactinia, and that the chromosomes are permanently attached to the central body and are thus brought side by side in nuclear fusion. On this ground he concludes that the chromosomes are permanent structures, and that they must be bivalent in the nuclei of the young ascus, due to the earlier fusion of the sexual nuclei. These bivalent chromosomes, he holds, further unite in synapsis to form quadrivalent structures, consisting of four somatic chromosomes arranged side by side, thus accounting for a numerical reduction just as in the higher plants. MAIRE says that the first division of the ascus nucleus is heterotypical, while the second is homeotypical, which opinion GUILLIERMOND also holds. HARPER gives no opinion as to which are the reduction divisions. He has pointed out, however, the universality of the occurrence of the double division, following synapsis in the spore mother cells of all higher plants, as necessary to accomplish chromosome reduction, where the chromosomes are bivalent structures. I might also call attention in this connection to the elimination of the double division in embryo sac mother cells of parthenogenetic angiosperms, discovered by JUEL (:00, :05), MURBECK (:01), OVERTON (:04), and STRASBURGER (:05), where reduction is not completed.

HARPER also points out that the universal triple division occurring in the ascus, no matter how many spores are to be formed, is probably to be associated with a quadrivalent character of the chromosomes in the ascus nucleus. Where one nuclear fusion occurs, as in most plants and animals, a double division is necessary to complete the reduction and to distribute the elements to the daughter nuclei; while when two nuclear fusions occur, as in Ascomycetes, a triple

division and a double reduction is necessary to accomplish the same results. This triple division of the ascus nucleus occurs universally, whether two spores, four spores, or eight spores are to be formed. HARPER has pointed out how fundamental this triple division is, since when only two spores are to be formed, as in Phyllactinia, six nuclei degenerate. In such cases the three divisions constitute a single continuous process. That all these divisions persist, no matter how many spores are to be produced, shows their necessity in the process of reduction.

The work of BLACKMAN (:**04**) and his students (:**06**) and of CHRISTMAN (:**05**) have established an undoubted alternation of generations in the rusts, showing that in these forms the series of binucleate cells originate as a result of fertilization. The gamete nuclei persist throughout the sporophyte generation as independent nuclei, dividing by a conjugate division. In the teleutospore these nuclei fuse, and a synapsis stage occurs, followed by a double division which leads to the formation of the four nuclei of the four sporidia. As HARPER suggests, there is a striking parallelism between the teleutospore and the spore mother cell of the higher plants. He believes we are justified in regarding the first and second divisions in the promycelium as respectively heterotypical and homeotypical. As there is only one nuclear fusion in the life cycle of the rust, a consequent double division occurs in reduction. MAIRE (:**05**), finding in Galactinia that certain of the cells of the ascogenous hyphae which give rise to the asci are binucleate, holds to the conception that these binucleate cells correspond to those of the Basidiomycetes as well as to those of the rusts. There should be a series of binucleate cells in the sporophyte in all these groups, whose nuclei should divide by conjugate division, fusion first taking place in the basidium, in the teleutospore, and in the ascus, each of which would be comparable to the spore mother cells of the higher plants. This explanation does not explain, however, the universal occurrence of the third division, which is so general among the Ascomycetes, and which FAULL has found to occur in the Laboulbeniaceae; nor does it account for the apparently secondary nature of the fusions described by BLACKMAN and CHRISTMAN, as compared to those of the red algae, lichens, mildews, and Pyronema. It is certainly of great importance to know

how the ascocarps of Galactinia, Acetabulum, and Pustularia arise, and whether apogamy or parthenogenesis is associated with the appearance of binucleate cells in the ascogenous hyphae.

The cells of the ascogenous hyphae of Thecotheus are not binucleate, and I am inclined to accept for this form HARPER'S interpretation that the asci are spore mother cells, modified by adaptation as explosive organs and as reservoirs of reserve food supply, in which a merely vegetative fusion has occurred to maintain a definite nucleocytoplasmic relationship. A triple division follows to complete the reduction and distribution of the somatic chromosomes to each of the resulting eight nuclei. The sporophyte would thus include the ascogenous hyphae and the asci up to the time of the reduction division, which initiates the gametophyte generation.

In the typical ascus the nuclei of the eight spores contain the gametophyte number of chromosomes, as would also be true when only two or four spores are formed. When any of these spores germinate, they give rise to true gametophyte structures, usually a septate mycelium, which may reproduce itself asexually by conidia before sexual reproduction, as in Eurotium or Erysiphe. It is well known that many ascospores contain more than one nucleus, and, as FAULL and others have shown, these nuclei are formed by mitotic division of the primary spore nucleus. The spore may be septate or non-septate. The typical ascospore is uninucleate and non-septate. Both the number of nuclei and the number of septa in a spore vary from one to many. Spores which are septate have apparently begun an intrasporal germination, the gametophyte forming considerable embryonic tissue within the old spore wall. Spores which are not septate but multinucleate have also undergone embryonic development, but without cell division.

We perhaps should expect from what we know of other Ascomycetes that in many-spored asci, as in Thecotheus and Ryparobius, spores would be delimited as soon as eight free nuclei were formed. This does not occur in either of these forms, but further nuclear divisions take place before the spores are delimited. A closer analysis, however, shows that we have analogies for these conditions in the behavior of other undoubted spore mother cells. Intrasporal germination may be looked upon as comparable to that which occurs in the

spores of many of the pteridophytes and spermatophytes. The spore not only begins its germination while inside the sporangium, but while it is still inside the mother cell. The ascus is not only to be looked upon as a mother cell, but also as a mother cell which functions directly as a sporangium. The prevalent impression is that the history of the gametophyte begins with the division of the mother cell and ends in the act of fertilization. The ordinary product of the division of the spore mother cell is four spores, or in typical Ascomycetes eight spores. In Lilium the first mitosis of the mother cell is heterotypical, while the second corresponds exactly in all details to the second division where normal tetrads are to be formed. We have here a double division completed inside the mother cell, and consequent germination to form a gametophyte inside the mother cell. It does not seem inconsistent, therefore, to think of a mother cell containing a gametophyte, or that the reduction divisions may not give rise directly to morphological spores. These nuclei are gametophytic in character and can give rise to gametophyte structures in the embryo sac. It is not absolutely essential, therefore, that the double division result in spore formation. JUEL (:00) found that in *Carex acuta* the usual double division occurs in pollen mother cells, complete cell plates being formed which are later resorbed, so that four nuclei lie inside the wall of the mother cell, three of which disintegrate, the fourth forming a single functional microspore. In Fuchsia (WILLE '86) as many as fourteen microspores have been reported from a single mother cell, while more or less than four have been found in several other forms. STRASBURGER and JUEL have also counted numerous microspores formed from a single mother cell. It would appear, therefore, that the double division is necessary, but that the number of spores ultimately formed is very variable. If in Fuchsia the walls of the microspores were eliminated, a striking resemblance to the sixteen-nucleate stage of Thecotheus would result. The number of spores formed and the time of their formation seems to be very variable, but this does not interfere with our conception of the alternation of generations in the flowering plants. That thirty-two free nuclei are formed in Thecotheus before spore delimitation occurs is therefore no more striking than that tetrads are not formed as a result of the double division in Lilium, or that more than four micro-

spores are formed in certain angiosperms. It may well be that all the conditions mentioned represent mere adaptations.

In the lichens many-celled spores occur, which are at first always uninucleate; for example, those of Endocarpon. The embryo gametophyte is formed in the spore, which continues its growth when conditions become favorable. Each cell, however, of the multinucleate septate spore gives rise to a filament when the spore germinates. Each cell of a septate spore is comparable to a spore of Thecotheus, in which walls have not been formed until the nuclear divisions have been completed. Germination occurs in the one case before spore delimitation, and in the other case after spore delimitation. In either case, after eight nuclei are formed we are dealing with gametophyte structures. It is a matter of indifference when germination occurs, or when spore delimitation takes place, so long as the triple division has occurred. The time of spore formation is a matter of adaptation to conditions, but the essential nature of the process seems to be the same in all genuine members of the group of Ascomycetes so far studied.

SUMMARY.

1. The fruit body of Thecotheus is formed from several ascogonia and is therefore a compound apothecium.

2. The ascogenous hyphae arise from any or all of the cells of the ascogonium, and consequently the cells of the ascogonium are not connected by perforations through which the nuclei pass to enter the ascogenous hyphae.

3. The ascogenous hyphae do not in this case constitute a synkaryophytic system.

4. The asci arise from the subterminal cells of the recurved tips of the ascogenous hyphae, which cells are binucleate.

5. The ascus nucleus is formed by the fusion of these two primary ascus nuclei.

6. The ascus nucleus divides by triple division to form eight free nuclei, each of which after a period of rest and growth undergoes further division until thirty-two free nuclei are formed in the ascus.

7. Spore delimitation follows the process described by HARPER.

8. Each spore is uninucleate from the start, no nuclear divisions or septa being formed.

9. The exospore is laid down not from the epiplasm but by deposition from the outer layer of the sporeplasm.

10. No evidence has been found to support the theory that the ascus is homologous with the sporangia of either the Oomycetes or the Phycomycetes.

11. The formation of the large number of spores is evidently an adaptive phenomenon, and does not interfere with the conception that the ascus is a spore mother cell.

UNIVERSITY OF WISCONSIN,
Madison, Wis.

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EXPLANATION OF PLATES XXIX AND XXX.

All drawings were made with the aid of a Bausch and Lomb camera lucida, together with a Bausch and Lomb $\frac{1}{12}$ oil-immersion lens. Plate XXX has been reduced one-third in reproduction.

PLATE XXIX.

FIG. 1. Section of young ascocarp showing portions of ascogonia, whose cells are already multinucleate.

FIG. 2. Median section of an older ascocarp showing ascogonia, young ascogenous hyphae, and paraphyses.

FIG. 3. Median vertical section showing structure of a nearly mature ascocarp.

FIG. 4. Section showing young ascogenous hypha; the terminal cell is uninucleate and the sub-terminal cell, which is to form the ascus, is binucleate.

FIG. 5. Young ascus showing fusion nucleus with two nucleoli.

FIG. 6. Portion of an ascus at time of spore delimitation, showing nuclear beak with a system of astral rays; a young spore is also shown, whose plasma membrane is completed.

PLATE XXX.

FIG. 7. Young ascus showing primary fusion nucleus with one nucleolus.

FIG. 8. Ascus with two nuclei.

FIG. 9. Ascus with four nuclei.

FIG. 10. Ascus with eight nuclei.

FIGS. 11a, 11b. Two sections of the same ascus, showing sixteen free nuclei, each of which will undergo another division to form thirty-two free nuclei.

FIGS. 12a, 12b, 12c. Three sections of the same ascus showing thirty-two young spores; *fig. 12a*, which is a median section, shows the arrangement of the spores about the ascus wall.

FIG. 13. Young spore showing early formation of spore wall.

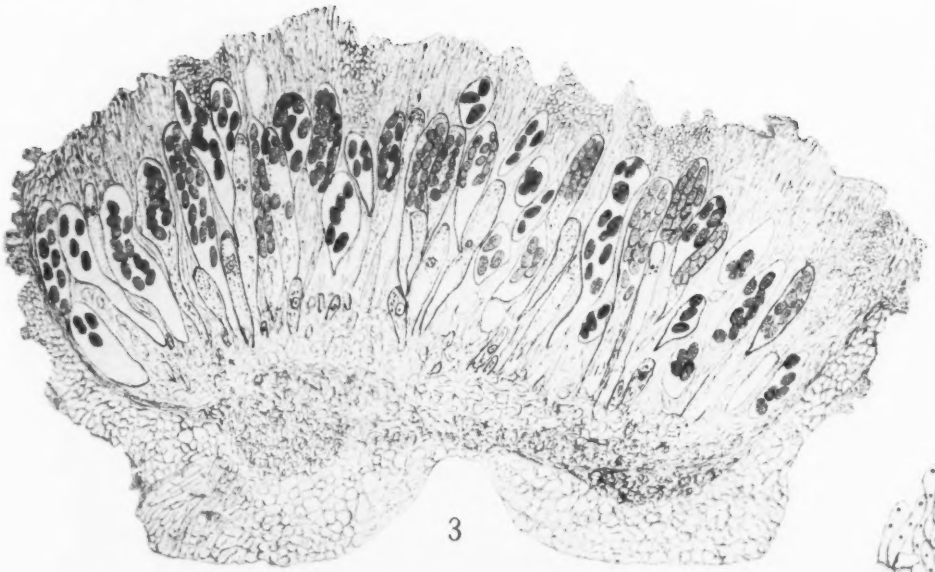
FIG. 14. Still older spore showing spore wall farther advanced.

FIG. 15. Mature spore showing spore wall, terminal pores, cytoplasm, and nucleus.

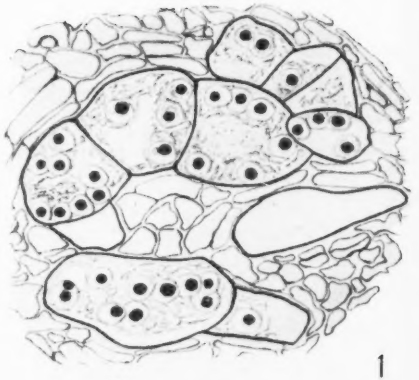
FIG. 16. Terminal portion of a nearly mature ascus showing operculum.

PLATE XXIX

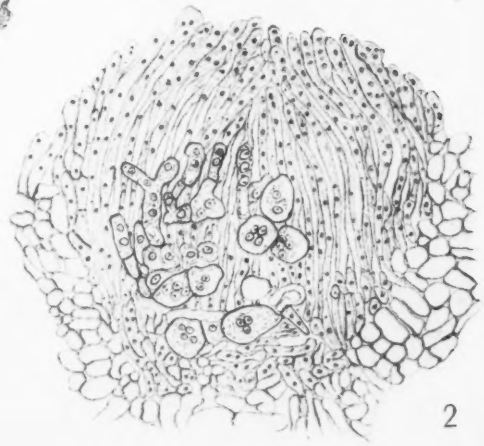
BOTANICAL GAZETTE, XLII



3



1



2

4

5

6

OVERTON on THECOTHEUS

8

7

9

10

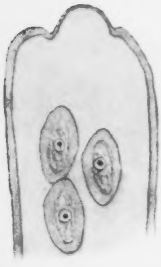
11b

11a

13

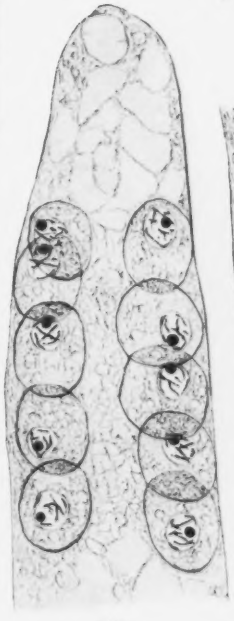
14

15

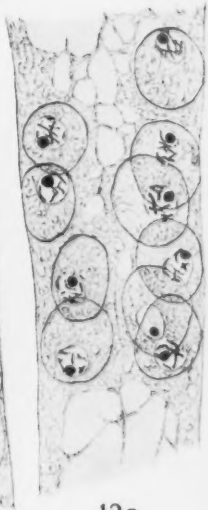


16

12b



12a



12c

OVERTON on THECOTHEUS

CURRENT LITERATURE.

BOOK REVIEWS.

The Vienna Congress.

THE PROCEEDINGS of the Congress of 1905 have recently appeared from the press of FISCHER (Jena), apparently published by the Local Committee.[1] At the same time there is published from the same house a volume containing the "scientific results" of the Congress as *Publications scientifiques de l'Association internationale des botanistes*.[2] The volumes have been distributed gratuitously to all members of the Congress, and are presumably for sale by the publisher; but the price is not stated.

The volume of *Verhandlungen* contains an account of the organization of the Congress and its daily proceedings in general sessions; the various excursions before and after the meetings; the botanical exposition (illustrated); but the greater part of the space (182 out of 262 pages) is devoted to an account of the meetings of the section for the revision of the laws of nomenclature. Here one finds not merely the *procès verbal*, but a list of the delegates and the institutions represented, an account of the discussions based on stenographic and other notes, and the votes on each question. Then follows, with double pagination, evidently for separate publication: (1) a concordance of the adopted rules with the Paris Code; (2) the revised code for the vascular plants, printed in French, English, and German; (3) a list of the names to be preserved as exceptions to the strict rule of priority; and (4) a thorough analytical index. This section of the report shows the painstaking care of M. JOHN BRIQUET, the general secretary, to whose devotion, skill, and knowledge so much of the success of the nomenclature commission was due.

[1] Verhandlungen des internationalen botanischen Kongresses in Wien 1905. Actes du congrès international de botanique à Vienne (Autriche) 1905. Herausgegeben im Namen des Organisations-Komittees für den Kongress von R. VON WETTSTEIN und J. WIESNER als Präsidenten und A. ZALHBRUCKNER als General-Sekretär. Redigiert VON J. BRIQUET (Genf), A. GINZBERGER, V. SCHIFFNER, TH. V. WEINZIRL, R. V. WETTSTEIN und A. ZAHLBRUCKNER (Wein). Imp. 8vo. pp. vi+262. *figs.* 7. Jena: G. Fischer. 1906.

[2] Publications scientifiques de l'Association internationale des botanistes. I. Résultats scientifiques du congrès international de botanique à Vienne, 1905. Wissenschaftliche Ergebnisse des internationalen botanischen Kongresses Wien 1905. Herausgegeben im Namen des Organisations-Komittees für den Kongress von R. VON WETTSTEIN und J. WIESNER als Präsidenten und A. ZALHBRUCKNER als General-Sekretär. Redigiert von P. J. LOTSY, General-Sekretär des Ass. Int. des Bot. Imp. 8vo. pp. vi+446. *pls.* 3. *map* 1. *figs.* 58. Jena: G. Fischer. 1906.

It seems a bit invidious to distinguish the other volume as *Résultats scientifiques;* but it may pass as a conventional title. The four hundred odd pages are occupied by the formal addresses, and papers volunteered for the Congress, twenty-six in number. They are therefore of unequal quality and of different character. Some are general summaries of the present status of important divisions of botanical science; others are special and technical. Only one comes from America—"A classification of Uredineae based on structure and development," by Dr. J. C. ARTHUR—and this is translated into German. The only English pages are those of Dr. D. H. SCOTT on "The fern-like seed-plants of the carboniferous flora." A good index makes available the entire contents. The two volumes should be in every botanical reference library.—C. R. B.

Knuth's Handbook.

In 1899 the first volume of KNUTH'S *Handbuch der Blütenbiologie* appeared,[3] based on HERMANN MULLER'S *Die Befruchtung der Blumen durch Insekten.* It is general and deals with the structure of flowers and of insects in relation to pollination. In the same year the second volume appeared,[4] giving an account of all known observations upon the pollination of the flowers of arctic and temperate zones. The third and last volume was published after the death of KNUTH, under the editorship of LOEW, and deals similarly with plants from countries other than Europe. The Clarendon Press has undertaken the publication of an English translation, the first volume of which has lately appeared,[5] and the second volume is announced as being in press. The translator is J. R. AINSWORTH DAVIS, Trinity College, Cambridge, and the prefatory note is by Professor I. B. BALFOUR.

The character of this encyclopedic work is well known to students of pollination, and it is a great boon to English and American botanists to possess it in an English translation. The original text appeared in instalments, and the appendices of supplementary information have been incorporated in the body of the text by the translator. A special feature of the translation is the bringing together in one list all the citations in the original, and completing the record to January 1, 1904. The number of citations is almost beyond belief, the botanical titles in the bibliographical list reaching 3748. It must be said, however, that the citations are probably more numerous than significant, as a cursory examination suggests. There are frequent cases where "fertilization" is confused with "pollination," and papers cited which can hardly be imagined as belonging to the real literature of pollination. Then too, there is occasional duplication of titles, as for example titles 633 and 643, which are identical in every particular. The dreadful task of editing such a mass of citations should

[3] BOT. GAZETTE **28**:280. 1899.

[4] BOT. GAZETTE **28**:432. 1899.

[5] KNUTH, PAUL, Handbook of flower pollination. Translated by J. R. AINSWORTH DAVIS. Volume I. 8 vo. pp. xix+382. Oxford: Clarendon Press. 1906.

excuse many slips, but the serious question is as to the value of such a mass of undigested citations.

In any event, the translation is exceedingly welcome, and should go far toward stimulating a study to which American botanists pay scant attention. —J. M. C.

A New Zealand Manual.

In 1864 Sir Joseph D. Hooker published the first part of his *Handbook of the New Zealand Flora*, which belonged to a uniform series of floras contemplated for all the British colonies. In 1894 the late Mr. T. Kirk was engaged by the New Zealand government to prepare a *Student's Flora* of New Zealand, but at his death in 1897 barely two-fifths of this task had been completed. This fragment has since been published by the government, but the need for a complete and convenient flora was becoming so acute that in 1900 Mr. T. F. Cheeseman, curator of the Auckland museum, was appointed by the government to prepare a *Manual of the New Zealand Flora*, and this has now appeared.[6]

The instructions to the author included one to follow the general plan of Hooker's *Handbook*, and another to include only indigenous plants. However, in an appendix the New Zealand families are arranged in the Engler and Prantl sequence; a list of the naturalized plants is also given, and a very long one it is. There is also an alphabetical list of Maori names of plants, and a full glossary. A most interesting and valuable contribution, contained among the introductory pages, is "A history of botanical discovery in New Zealand," from Cook's first visit in 1769 to the present year.

As is customary, only the vascular plants are included, and the range covered includes not only the two main islands of the Colony of New Zealand, but also the outlying groups of the Kermadec Islands, the Chatham Islands, the Auckland and Campbell Islands, Antipodes Island, etc. Macquarie Island is also included, although it belongs to Tasmania, because it is more closely allied in its flora to the Auckland and Campbell Islands than to any other land. The descriptions are in almost all cases original, and have been based upon the examination of living or dried material, extending through thirty-five years of continuous study and collection of the flora. Surely no one of larger experience could have been selected to do this work, which gives evidence throughout of most painstaking care and most orderly and clear presentation.

The composition of this flora makes it one of the most interesting on the globe, and hence a few general data concerning it will not be out of place. The volume includes the descriptions of 1571 species, only 156 of them being pteridophytes. The four largest families, with species numbering from 221 down to 113, are Compositae, Cyperaceae, Scrophulariaceae, and Gramineae; and the Compositae constitute one-seventh of the whole flora. The largest genus is Veronica,

[6] Cheeseman, T. F., Manual of the New Zealand Flora. 8vo. pp. xxxvi+1199. Wellington: Published under the authority of the Government of New Zealand. 1906.

with 84 species, followed by Carex, Celmisia (Compositae), Coprosma (Rubiaceae), Ranunculus, Olearia (Compositae), etc. Numerous new species are described and a new genus (*Townsonia*) of Orchidaceae is established. The most remarkable fact is that of the 1571 species 1143 are endemic, nearly three-fourths of the entire flora. Of the 428 species found elsewhere, 366 extend to Australia, and 108 to South America. This almost complete "strangeness" of the flora to botanists who are familiar with the north temperate floras and who have even visited the tropics, gives it a fascination suggestive of just as strange results if such material could be made available in their laboratories.—J. M. C.

MINOR NOTICES.

Development of fern leaves.—MARGARET SLOSSON has brought together in an elaborate book a remarkable series of observations upon the development of fern leaves.[7] She has selected nineteen representative species from northeastern United States, and illustrated them by forty-six handsome plates reproduced from photographs. A preliminary chapter contains a general description of the development of form and venation, often showing remarkable changes in passing from the juvenile to the mature form. In the subsequent chapters each species is first described in its mature form, and then follows a very detailed description of the transition forms from the juvenile stage. The possible range of leaf variation is also considered. The book contains a mass of suggestive observations, which should serve as a check to any characterization of species from insufficient material, and as a demonstration that the numerous "form species" of fossil "ferns" are more than doubtful. The book is more of a contribution than its elaborate form would suggest.—J. M. C.

Portraits of botanists.—DÖRFLER, editor of *Botaniker-Adressbuch*, has issued the first two parts of a proposed series of portraits of botanists. Each part contains ten portraits, 9×12.5^{cm}, which are phototype reproductions upon fine art cards, each card also bearing the signature of the botanist in facsimile. The cards are loose, being ready to frame and worthy of it. It is announced that 100 portraits, with title page and index, will form a volume. A grape of text accompanies each portrait, giving the most important biographical data and bibliography. Each part costs 5 marks to subscribers; single portraits can be obtained for 1 mark; and 10 selected portraits for 8 marks. The first part contains portraits of KERNER, WIESNER, WARMING, ENGLER, DEVRIES, GUIGNARD, SCHRÖTER, MATTIROLO, WILLE, and WETTSTEIN; the second part, FRIES, (Elias and Theodor), PFEFFER, BORODIN, HACKEL, SCOTT, GOEBEL, ERRERA, CHODAT, and IKENO. The address is J. DÖRFLER, Barichgasse 36, Wien, III.—J. M. C.

[7] SLOSSON, MARGARET, How ferns grow. 8vo. viii+156. New York: Henry Holt & Company. 1906.

Ustilaginales of the North American Flora.—Another part of the *North American Flora* has appeared, containing the Ustilaginales by CLINTON.[8] The changes from a former monograph[9] by the same author are mostly such as adapt the monograph to the style of the *Flora*. The older European synonomy, the list of species showing general distribution, and the extensive bibliography of the former publication are omitted. The omission of the general notes relating to the genera and species is a distinct disadvantage. It takes away from the descriptions all that individuality which helps the mind to recognize a plant from its description far more readily than do the technical diagnoses. The host index in its present alphabetical arrangement of hosts, with page references to the parasites, represents a marked improvement over the former arrangement. Artificial keys for the determination of species have been added under the genera. —H. HASSELBRING.

Index Filicum.—This work is completed by the twelfth fascicle[10], which concludes the catalogue of literature, and also includes a systematic enumeration of the genera. It appears that 23,499 names are cited, but that only 149 generic names and 5940 specific names stand. It is interesting to note that these species are distributed among the 12 families as follows: Hymenophyllaceae 462, Cyatheaceae 456, Polypodiaceae 4527, Parkeriaceae 1, Matoniaceae 2, Gleicheniaceae 80, Schizaeaceae 118, Osmundaceae 17, Salviniaceae 18, Marsileaceae 63, Marattiaceae 118, Ophioglossaceae 78. This sequence of families is that used by the author. The parts have appeared with most commendable promptness, and the completed volume will be a most useful one.—J. M. C.

Trees of the Amazon region.—HUBER has issued the third and fourth decades of his *Arboretum Amazonicum*,[11] the first two parts having appeared in 1900.[12] The superb quality of the plates is maintained, and, as before, each plate is accompanied by at least a page of descriptive text in Spanish and French in parallel columns. There are habit studies of different palms, legumes, etc., views of different types of savannas, characteristic river-bank vegetation, forest interiors, effect of wind on trees, etc. These glimpses of tropical plants and plant formations are among the very finest that have been published.—J. M. C.

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[8] CLINTON, G. P., Ustilaginales. North American Flora **7**: part 1. pp. 82. October 4, 1906.

[9] North American Ustilaginaeae. Proc. Boston Soc. Nat. Hist. **31**:329-529. 1904. Reviewed in BOT. GAZETTE **39**:314. 1905.

[10] CHRISTENSEN, C., Index Filicum, etc., Fasc. 12. Copenhagen.: H. Hagerup. 1906. 3*s*. 6*d*.

[11] HUBER, J., Arboretum Amazonicum. Iconographie desplantes spontanées et cultivées les plus importantes de la région Amazonienne. Decades 3 and 4. 4to. Para. 1906. Each decade 10 fr.

[12] BOT. GAZETTE **33**:72. 1902.

Ptelea.—A revision of this genus as it occurs in western and southwestern United States and Mexico has been published by GREENE.[13] Under his treatment the genus has become rich in species, 59 being recognized, of which 55 are new. Three natural groups are defined, each with its own geographical range: (1) species (37) with chestnut-brown twigs and prevailingly glaucescent or bluish-green foliage; (2) species (13) with amost white twigs and yellow green foliage; (3) species (9) with cinnamon-colored twigs, a peculiar hue and venation of foliage, and narrow-winged or even wingless samaras.—J. M. C.

Anatomy of Commelinaceae.—HOLM has published an elaborate memoir[14] dealing chiefly with the general morphology and anatomy of the Commelinaceae. The 17 species investigated represent the genera Commelina (5), Aneilema, Tinantia, Tradescantia (9), and Weldenia. The memoir is a mine of information which can be drawn upon by the future student of the group who is seeking to organize such details into general statements.—J. M. C.

Genera Siphonogamarum.—The eighth fascicle of DALLA TORRE and HARMS'S[15] list of the genera of seed plants concludes the genera of Compositae, 9629, Thamnoseris being the last one. The genera of uncertain affinity swell the number of genera to 9810. There is also a supplement of 51 pages, and the general index of names is begun.—J. M. C.

NOTES FOR STUDENTS.

Ancient Araucarians.—In Jurassic and Cretaceous deposits there occur abundant remains of leafy branches of coniferous plants that have been described under the generic name Brachyphyllum. The genus has been referred by various authors to Araucarineae, to Cupressineae, and to Taxodineae (near Sequoia); but in a recent paper by JEFFREY and HOLLICK[16] it is shown from an investigation of the internal structure that here can be no doubt as to its Araucarian affinities. In the same paper *Protodammara* is described as a new genus, to include certain Cretaceous cone scales that had been referred to the living genus Agathis (Dammara). Certain lignites associated with both Brachyphyllum and Protodammara were also found to be Araucarian; and the conclusion is reached that these lignites represent the wood of the trees which bore the leafy

[13] GREENE, EDWARD L., The genus Ptelea in the western and southwestern United Stated and Mexico. Contrib. U. S. Nat. Herb. **10**:49–79. 1906.

[14] HOLM, THEODORE, Commelinaceae. Morphological and anatomical studies of the vegetative organs of some North and Central American species. Memoirs Nat. Acad Sci. **10**:159–192. *pls. 1–8.* 1906.

[15] DALLA TORRE, C. G. DE and HARMS, H., Genera Siphonogamarum ad systema Englerianum conscripta. Fasc. 8. pp. 561–640. Leipzig: Wilhelm Engelmann. 1906. *M6.*

[16] HOLLICK, A., and JEFFREY, E. C., Affinities of certain Cretaceous plant remains commonly referred to the genera Dammara and Brachyphyllum. Amer. Nat. **40**: 189–215. *pls. 1–5.* 1906.

branches called Brachyphyllum and the cones called Protodammara. This multinomial genus was thought by the authors to be "in all probability the last survivor of an ancient Araucarian line of descent, joined near its base with the primitive stocks of the Abietineous and Cupressineous series."

More recently JEFFREY has been able to study the wound reactions of Brachyphyllum and to draw from them more definite conclusions as to its relationships.[17] In a well-preserved specimen of the wood, Brachyphyllum can be distinguished at once from any living Araucarian by the absence of resiniferous elements other than those found in the pith-rays. In this feature the genus resembles such old gymnosperm groups as the Pteridospermae, Cordaitales, and Cycadales, and also the very ancient but still flourishing genus Pinus. JEFFREY further finds that Brachyphyllum agrees with the Abietineae in its traumatic reactions, resin-canals being formed as a result of wounding. Following the line of reasoning used in connection with his work on Sequoia,[18] he concludes that these reactions furnish one evidence that the Araucarieae are phylogenetically connected with the Abietineae; and that Agathis and Araucaria hold the same relation to Brachyphyllum that the other genera of the Cupressineae hold to Sequoia. This phylogenetic linking together of both the Cupressineae and Araucariaeae with the very ancient Abietineae is especially interesting on account of the very isolated position of existing Araucarians among existing Coniferales, and also on account of SEWARD's recently expressed views[19] in reference to the relationships and origin of the Araucarians.—J. M. C.

Adsorption of chlorophyll.—It has always been troublesome to explain the differential extraction of the chlorophyll pigments by their solvents under various conditions, and TSWETT seeks to supply a better theory.[20] Thus, fresh leaves or those ground in a mortar with sand or emery and covered with petrolether yield a more or less pure-yellow extract of carotin, with traces of other pigments. Dried leaves, even at a lower temperature, yield even purer carotin. But boiled leaves, or even warmed tissues, yield green extract. Alcohols (methyl, ethyl, and amyl), acetone, acetaldehyde, ether, and chloroform give a green extract with fresh, dry, or boiled leaves, dissolving all pigments freely. It suffices to add a little alcohol (10 per cent. for fresh, 1 per cent. for dry leaves) or the other solvents to petrolether to secure a beautiful green extract. How explain these facts?

If strips of filter paper be put into a flask with an alcohol-petrolether solution and the solvent evaporated *in vacuo*, the pigments become concentrated in the paper. This dry green paper now behaves toward solvents exactly as above stated for the green leaves. This, TSWETT holds, indicates that the pigments[23]

[17] JEFFREY, E. C., The wound reactions of Brachyphyllum. Annals of Botany **20**:383–394. *pls. 27–28.* 1906.

[18] See BOT. GAZETTE **38**:321. 1904.

[19] See BOT. GAZETTE **42**:224. 1906.

[20] TSWETT, M., Physikalisch-chemische Studien über das Chlorophyll. Die Adsorptionen. Ber. Deutsch. Bot. Gesells. **24**:316–23. 1906.

are absorbed by the stroma, i. e., held mechanically by molecular affinity, and in different degrees under different conditions, this molecular attraction being overcome by the various solvents unequally. Consequently, it is argued, the pigments cannot exist as grana in the stroma—a conclusion already indicated by recent study both with microscope and ultramicroscope. Many bodies beside cellulose hold the pigments in like fashion. The work is suggestive, but TSWETT'S crucial experiment is not convincing.

Inasmuch as the different pigments are held fast unequally, if a petrolether solution, or even better a solution in carbon bisulfid, be filtered through a column of calcium carbonate, the pigments are distributed in zones, the more firmly adsorbed ones above, the less firmly fixed successively lower. Such a preparation he calls a chromatogram, and the method the chromatographic method.[21]

In a later paper[22] TSWETT gives further details of the technique and analyzes the zones of his chromatogram. The synonymy of the chlorophyll pigments is so tangled that it is almost impossible to compare the work of different investigators. The chromatographic method promises to be of use in demonstrating that there are different pigments, but its value in research seems questionable. —C. R. B.

The Svalöf Experiment Station.—Although the work of the Swedish Agricultural Experiment Station at Svalöf is widely celebrated because of its noteworthy economic results, these results and the means by which they have been attained are not generally understood, owing to the fact that all of its reports are printed in the Swedish language. DE VRIES has devoted two recent papers[23] to a discussion of the Svalöf methods and their scientific significance. In the first of these papers is given a brief history of the station, together with an exposition of the methods employed. The history of the station falls rather naturally into four 5-year periods, each marked by a characteristic advance. During the first period, 1886–1891, the work of introduction and testing of varieties, in the way usually done by Agricultural Experiment Stations, presents nothing unique, the several sorts being treated as units. With the appointment of Dr. H. NILSSON as Director in 1890 begins the second period, in which the discovery was made that each variety is a mixture of a large number of elementary forms and that the latter are the real units with which scientific agriculture must deal. In the third period was carried out the great work of segregating the elementary

[21] TSWETT proposes to call the collective green pigment of leaves chlorophyll; the green fluorescent components chlorophyllins; the yellows already are distinguished as carotins and xanthophylls.

[22] TSWETT, M., Adsorptionsanalyse und chromatographische Methode. Anwendung auf die Chemie des Chlorophylls. Ber. Deutsch. Bot. Gesells. **24**:384–393. 1906.

[23] DEVRIES, HUGO, Die Svalöfer Methode zur Veredelung landwirthschaftlicher Kulturgewächse und ihre Bedeutung für die Selektionstheorie. Arch. für Rass. u. Gesells.-Biol. **3**:325–358. My-Je 1906.

Altere und neuere Selektionsmethode. Biol. Centralbl. **26**:385–395. Jy 1906.

forms, studying their morphological characters, and testing their relative value by parallel cultures. During the last five years the successive generations of these segregated pure races have been followed, with the result that a considerable number of mutants have been found and tested. In both papers DEVRIES compares NILSSON'S pedigree-culture method with the older and still almost universal method of selection in which the undesirable individuals are destroyed and all the best are saved and sown together. He concludes that RIMPAU could have produced the Schlanstedt barley, for which he is so widely celebrated, in four or five years by the Svalöf method, instead of having to devote to it the 20–25 years required by the older method. The magnitude and quickness of the results at Svalöf, where alone the conception of constant elementary forms has been adopted as the basic principle, indicates the importance of the newer conceptions of evolution for scientific agriculture, and these papers of DEVRIES bring to the notice of the non-Swedish world methods which will doubtless lead to most important changes in the conduct of the various agricultural stations.—GEO. H. SHULL.

Report to Evolution Committee.—In a third report to the Evolution Committee of the Royal Society, BATESON, SAUNDERS, and PUNNETT[24] have shown that practically all the complexities encountered in their study of hybrid stocks, sweet peas, and poultry are in essential accord with Mendelian expectation if the assumption is made that what appears externally as a single character may be in reality dependent for its appearance upon the presence of two or more independent allelomorphs or internal units. In some cases the nature of these internal units is apparent, as when the presence of one always changes a pigment from red to blue; but in other cases there is no clue to the nature of the individual allelomorph, as when the combination of two white sweet peas invariably produce colored offspring owing to the bringing together of two allelomorphs the combined action of which is necessary to the production of color. In stocks the presence of hoary pubescence is shown to depend upon the simultaneous presence of four independent allelomorphs, two of which are also necessary to the production of colored flowers. At the New Orleans meeting of the Botanical Society of America (December 1905) the reviewer presented a paper on the "Latent characters of a white bean," in which it was shown that the color of purple mottled beans obtained as an F_1 from a cross between yellow and white is dependent upon the simultaneous presence of three distinct allelomorphs. In that paper it was predicted that BATESON'S results on stocks and sweet peas would find a satisfactory explanation on the same grounds without the assumption of complex and inexplicable synthesis and resolution of "hypallelomorphs" as attempted in the earlier Reports to the Evolution Committee. The completeness with which the new point of view is demonstrated by these further investigations will do much to strengthen the view that Mendelian behavior is a more common

[24] BATESON, W., SAUNDERS, Miss E. R., PUNNETT, R. C., Reports to the Evolution Committee. III. pp. 52. London: Harrison & Sons. 1906.

phenomenon than previous observations would have indicated. Although stocks behave in a rather simple way when the analysis given by the authors is comprehended, the recombination of the allelomorphs that have been discovered in this plant yields in the second generation 243 distinct types, and it is plain that in still more complex cases a perfectly typical Mendelian behavior would easily exceed the keenest human power of analysis to unravel.—GEO. H. SHULL.

Sterilized soil.—SCHULZE finds[25] that plants grown in sterilized soil are affected by two opposing factors: (1) the formation of more or less injurious decomposition products in the sterilizing process, which act upon the plants "according to the degree of their sensitiveness" (this phrase obviously hides ignorance of other factors); (2) an advantageous release of nutritive materials, especially of the otherwise unavailable nitrogen. According as one or the other of these factors prevails the crop is increased or diminished by sterilizing the soil. But even when the crop is diminished the N-content may be markedly increased. By the addition of lime the injurious effect of the decomposition products may be almost or wholly counteracted. The significance of these researches for pot-cultures in sterilized soil is obvious, invalidating many conclusions based upon such experiments when this factor had not been considered.—C. R. B.

Moss rhizoids.—KURT SCHOENE finds[26] that rhizoids rarely arise from the germinating spores of any mosses except Funaria, in which they regularly appear. Lack of nitrogen suppresses the chloronema of Funaria, reducing it much in others; and lack of either nitrates or phosphates enormously lengthens the rhizoids of Funaria. These peculiarities of spore germination mark Funaria as a ruderal plant. The rhizoids show a gradation in their significance as organs of food supply, diminishing from the forms with a central strand to those without it, this function entirely disappearing in water forms. (The experiments on which this statement rests are too few and inconclusive to be convincing.) The oblique position of partitions is held to be a mechanical arrangment for resisting longitudinal strains and too great deformation of plasma on bending. It is not obvious that in nature such dangers often threaten.—C. R. B.

Items of taxonomic interest.—OAKES AMES (Proc. Biol. Soc. Washington **19**:143–154. 1906) has described 18 new species of Acoridium (Orchidaceae) from the Philippines.—R. SCHLECHTER (Bull. Herb. Boiss. II. **6**:843. 1906), in Loesener's *Plantae Selerianae*, has described a new genus (*Labidostelma*) of Asclepiadaceae from Guatemala.—C. B. CLARKE (Kew Bull. 1906:251) has published a new African genus (*Crossandrella*) of Acanthaceae.—A. D. E. ELMER (Leaflets on Philipp. Bot. **1**:42–73. 1906) has published new Philippine species under Pandanus (2), Ficus (8), and the Rubiaceae (14).—J. M. C.

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[25] SCHULZE, C., Einige Beobachtungen über die Einwirkung der Bodensterilisation auf die Entwickelung der Pflanzen. Landw. Versuchs-Stat. **65**:137–147. 1906.

[26] SCHOENE, KURT, Beiträge zur Kenntnis der Keimung der Laubmoossporen und zur Biologie der Laubmoosrhizoiden. Flora **96**:276–321. 1906.

NEWS.

CHESTER A. DARLING, Albion College (Mich.), has been appointed assistant in botany at Columbia University.

DR. ALBERT MANN, Department of Agriculture, has been appointed professor of botany at George Washington University.

A BIOGRAPHICAL SKETCH, with portrait, of the late C. B. CLARKE is published in *Journal of Botany* for November, having been prepared by D. PRAIN and W. H. BLISS.

PROFESSOR L. H. BAILEY, Cornell University, was elected president of the Association of Agricultural Experiment Stations at the recent Baton Rouge meeting.

MR. A. C. SEWARD, formerly university lecturer, has been elected to the professorship of botany at Cambridge made vacant by the death of Professor H. MARSHALL WARD.

PROFESSOR ROLAND THAXTER, Harvard University, has returned from his year's leave of absence. A portion of his time was spent in South America and included a collecting trip to the Straits of Magellan.

THE DATE of publication of the November GAZETTE should have been given as November 30 instead of November 17. After the number was printed publication was delayed by unforseen difficulties with the plates, due to a lithographer's strike.

IN CONNECTION with the recent quatercentenary celebrations of the University of Aberdeen, honorary degrees were conferred on the following botanists: CASIMIR DECANDOLLE, Geneva; HUGO DEVRIES, Amsterdam; J. MATSUMURA, Tokyo; and D. H. SCOTT, Kew.

IT IS appropriate to call attention again to the limitations which the Editors have been obliged to establish for papers published in the GAZETTE. No article exceeding thirty-two pages is acceptable, except with the consent of the author to pay for the pages in excess of thirty-two, which will be added to the usual number.

THE DEPARTMENT OF AGRICULTURE, in its Yearbook for 1905, publishes a paper on the progress of forestry during that year. The year is regarded as "an epoch in the history of American forestry," chiefly because during that year it "passed out of the stage of preparation and propaganda into that of actual work." On February 1, 1905, the administration of the national forest reserves came under the Department of Agriculture, and by the end of that year an efficient system of forest administration was being inaugurated upon a hundred million acres of forest lands.

THE ROYAL SOCIETY of London has awarded recently the following medals to botanists: A Royal medal to Dr. D. H. SCOTT for his investigations and discoveries in connection with the structure and relationship of fossil plants; the Darwin medal to Professor HUGO DEVRIES on account of the significance and extent of his experimental investigation in heredity and variation.

THE FIRST SESSION of the next annual meeting of the American Association will be held at Columbia University on the morning of Thursday, December 27. During Thursday and Friday Section G will meet at Columbia University; but on Saturday it will meet in connection with the Botanical Society of America at the New York Botanical Garden. The meetings will continue on Monday and Tuesday, or as long as is required by the program.

THE UNIVERSITY OF CALIFORNIA has received by donation the herbarium and botanical library of Mr. and Mrs. T. S. BRANDEGEE, of San Diego. The herbarium is one of the most important in the west, since it contains something over 100,000 sheets of carefully selected plants, mostly representative of the Mexican flora, which for many years has been Mr. BRANDEGEE's chosen field, and of the flora of California and neighboring states, which has received careful treatment at the hands of Mrs. BRANDEGEE. It contains the sole remaining duplicate types of many species, the originals of which were lost in the recent fire that destroyed so large a portion of the herbarium of the California Academy of Sciences as well as the types of practically all the new species described by Mr. and Mrs. BRANDEGEE themselves. Among the noteworthy sets represented are BEBB's willows, PARRY's Manzanitas and Chorizanthes, a majority of the Mexican sets distributed by PALMER, PRINGLE, LUMHOLTZ, PURPUS, etc., and a selection of types and duplicate types from the ORCUTT and CLEVELAND herbaria. It is probable that no other herbarium contains so nearly complete a representation of the North American Borraginaceae. It is also rich in Mimulus, Eriogonum, and other groups in which Mrs. BRANDEGEE has been particularly interested.

The University Herbarium, as now enlarged, numbers approximately 250,000 sheets, a majority of which are mounted in permanent form. The whole collection is available for study and occupies fire-proof quarters in one of the buildings recently erected on the University campus. Here visiting botanists desiring to study the West American and Mexican flora or to consult the working library of the herbarium, will be welcome and given every opportunity for research work. Mr. and Mrs. BRANDEGEE will continue their studies at the University where Mr. BRANDAGEE has been appointed Honorary Curator of the Herbarium. Mail matter may hereafter be addressed to them at the University.

GENERAL INDEX.

The most important classified entries will be found under Contributors, Personals, and Reviews. New names and names of new genera, species, and varieties are printed in **bold-face** type; synonyms in *italic*.

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